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Memory as the "whole brain work" A large-scale model based on "oscillations in super-synergy"

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Abstract

According to recent trends, memory depends on several brain structures working in concert across many levels of neural organization; *memory is a constant work—in progress*." The proposition of a brain theory based on super-synergy in neural populations is most pertinent for the understanding of this constant work in progress.

This report introduces a new model on memory basing on the processes of EEG oscillations and Brain Dynamics. This model is shaped by the following conceptual and experimental steps:

1. The machineries of super-synergy in the whole brain are responsible for formation of sensory–cognitive percepts.
2. The expression "*dynamic memory*" is used for memory processes that evoke relevant changes in alpha, gamma, theta and delta activities. The concerted action of distributed *multiple oscillatory processes* provides a major key for understanding of *distributed memory*. It comprehends also the phyletic memory and reflexes.
3. The evolving *memory*, which incorporates reciprocal actions or reverberations in the *APLR alliance* and during *working memory processes*, is especially emphasized.
4. A new model related to "*hierarchy of memories as a continuum*" is introduced.
5. The notions of "*longer activated memory*" and "*persistent memory*" are proposed instead of long-term memory.
6. The new analysis to recognize faces emphasizes the importance of EEG oscillations in neurophysiology and Gestalt analysis.
7. The proposed basic framework called "*Memory in the Whole Brain Work*" emphasizes that memory and all brain functions are inseparable and are acting as a "*whole*" in the whole brain.
8. The role of genetic factors is fundamental in living system settings and oscillations and accordingly in memory, according to recent publications.
9. A link from the "*whole brain*" to "*whole body*," and incorporation of vegetative and neurological system, is proposed, EEG oscillations and ultraslow oscillations being a control parameter.

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Keywords: Brain oscillations; Memory; Theta; Alpha; Gamma; Matching; Brain function; Superbinding

1. Introduction

The major aim of this report is the introduction of a "*memory model based on EEG oscillations*." This construct is new, since nobody has yet tried to link the commonly accepted memory model with new results that emerged from brain dynamics. Therefore, this "*fresh construct*" is subject

Abbreviations: AFC, amplitude frequency characteristics; ERO, event-related oscillation; APLR, alliance of attention, perception, learning and memory.

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to alterations and extensions in future. Such constructs are needed, since the EEG oscillations attract considerable attention in neuroscience.

There are also new tendencies to unify perception, learning and remembering processes, in several levels: Baddeley's (1996) new scope on working memory provides the interface of perception, attention, memory, and action. Single cell analysis of R. Desimone (1996) underlines the same view at the physiological level. New strategies to consider event-related EEG oscillations (Population of neurons) as an alliance of attention, perception, learning and remembering (*APLR alliance*) had been undertaken by Başar (2004), who applied the concepts of Fuster (1995, 2003) and Hayek (1952) and considered memory as an entity inseparable from other brain functions.

Important steps of this article are:

1. The introduction of "*physiological memory*"
2. The emphasis of "*evolving memory*," which incorporates reciprocal actions or reverberations in the *APLR alliance* during *working memory process*
3. The introduction of "*hierarchy of memories as a continuum*"
4. The use of "*longer acting memory*" instead of "*long-term memory*"
5. A proposal to emphasize physiological settings and "ultraslow myogenic oscillations" in order to link the neurological and vegetative functions and to incorporate the whole brain and the whole body.

1.1. Emphasis of multiple oscillations in brain research

As Mountcastle (1992) and Freeman (1999) state, neuroscience is ripe for a change. Accordingly, in the last decade, an increasing number of reports and reviews on "electrical oscillations in the brain" were encountered in neuroscience literature. However, only a few of them point out the importance of multiple oscillations. In order to fill this gap, this paper has the goal of embracing oscillations related to sensory and cognitive processing in all frequency channels by using human and animal recordings. Moreover, new results are included to emphasize the role of oscillatory dynamics in the coordination of function with the circulatory system, lymphatic system and the overall myogenic system controlling peristalsis and all visceral organs in the "*ultra-slow frequency range*" (Başar and Weiss, 1981).

The functional importance of distributed multiple oscillations in the brain was for the first time emphasized in a series of reports in the 1970s (Başar, 1992; Başar et al., 1975a,b,c), Başar and Ungan, 1973). *Long-distance coherences* in the brain were also already demonstrated by Başar (1980) and Başar et al. (1979a,b).

The principle of superposition describes integration over the temporal axis consisting of a relationship between the amplitude and phases of oscillations in various frequency bands. Furthermore, selectively distributed and selectively coherent oscillatory activities in neural populations describe integration over the spatial axis (Başar, 1980). Consequently, integrative activity is a function of the coherences among spatial locations of the brain; these coherences vary according to the type of sensory and/or cognitive event and possibly the state of consciousness of the species (Başar, 1999, 2004). The publications of Bressler and Kelso (2001), Von Stein and Sarnthein (2000) and Varela et al. (2001) clearly describe this trend in which the concerted activity of alpha, theta, and delta and beta oscillations in distributed structures as reticular formation (RF), hippocampus (HI), thalamus and sensory cortices was emphasized.

1.2. What is the role of oscillations in memory processing?

The experimental work of Klimesch group shows the possibility of differentiating the role of alpha and theta oscillatory activity during memory tasks. The results from this group support the hypothesis that ERPs can be understood and described in terms of superpositions of several event-related oscillations recorded in various structures (Klimesch et al., 2000a,b; Doppelmayer et al., 2000). Moreover, their experiments include memory tasks differentiating oscillatory responses of good and bad memory performers.

According to Fuster's (1997) view, *memory reflects* a distributed property of cortical systems. An important part of higher nervous function, as perception, recognition, language, planning, problem solving and decision-making, is interwoven with memory. Memory is a property of the neurobiological systems it serves and is inseparable from their other functions. By surveying the data presented in this section, it can be hypothesized that the selectively distributed oscillatory systems (or networks) may provide a general communication framework and can be a useful concept for functional mapping of the brain (Mesulam, 1990, 1994). New experimental designs as the experiments by the groups of (Burgess and Gruzelier, 2000; Egner and Gruzelier, 2001; Haenschel et al., 2000; Klimesch, 1999; Klimesch et al., 1994) are extremely important, for they add new steps to the general framework of function-related oscillations.

2. Selectively distributed oscillatory systems in brain function: distributed multiple oscillations in brain

According to the new trend, the EEG consists of the activity of an ensemble of generators producing rhythmic activity in several frequency ranges. These oscillators are active usually in a random way. However, by application of sensory stimulation, these generators are coupled and act together in a coherent way. This synchronization and enhancement of EEG activity give rise to "evoked" or "induced rhythms." Evoked potentials representing ensembles of neural population responses were considered as a result of transition from a *disordered* to an ordered state. The compound ERP manifests a *superposition* of evoked oscil-

lations in the EEG frequencies ranging from delta to gamma ("*natural frequencies of the brain*" such as alpha: 8–13 Hz, theta: 3.5–7 Hz, delta: 0.5–3.5 Hz and gamma: 30–70 Hz). The correlates of EEG oscillations at the cellular level gained tremendous importance following the studies of Singer (1989).

Time-locked responses of a specific frequency after stimulation can be identified by computing the amplitude frequency characteristics (AFCs) of the averaged ERPs (Başar, 1980; Röschke et al., 1995; Kolev and Yordanova, 1997). The AFC describes the brain system's transfer properties, e.g., excitability and susceptibility, by revealing resonant as well as salient frequencies. It therefore does not simply represent the spectral power density characterizing the transient signal in the frequency domain but the predicted behavior of the system (brain) if sinusoidally modulated input signals of defined frequencies were applied as stimulation. As reflecting the amplification in a given frequency channel, the AFC is expressed in relative units. Hence, the presence of a peak in the AFC reveals the *resonant frequencies* interpreted as the most preferred oscillations of the system during response to a stimulus. To calculate the AFCs, ERPs were first averaged and then transformed to the frequency domain by means of one-sided Fourier Transform (Laplace transform, see Solodovnikov, 1960; Başar, 1980).

An AFC is illustrated in Fig. 1, demonstrating that auditory stimuli produce prominent resonant responses in the theta, alpha, and gamma (40 Hz) frequency bands in the cat hippocampus (from Başar, 1980). The AFCs serve also to define filter limits for response-adaptive digital filtering of the

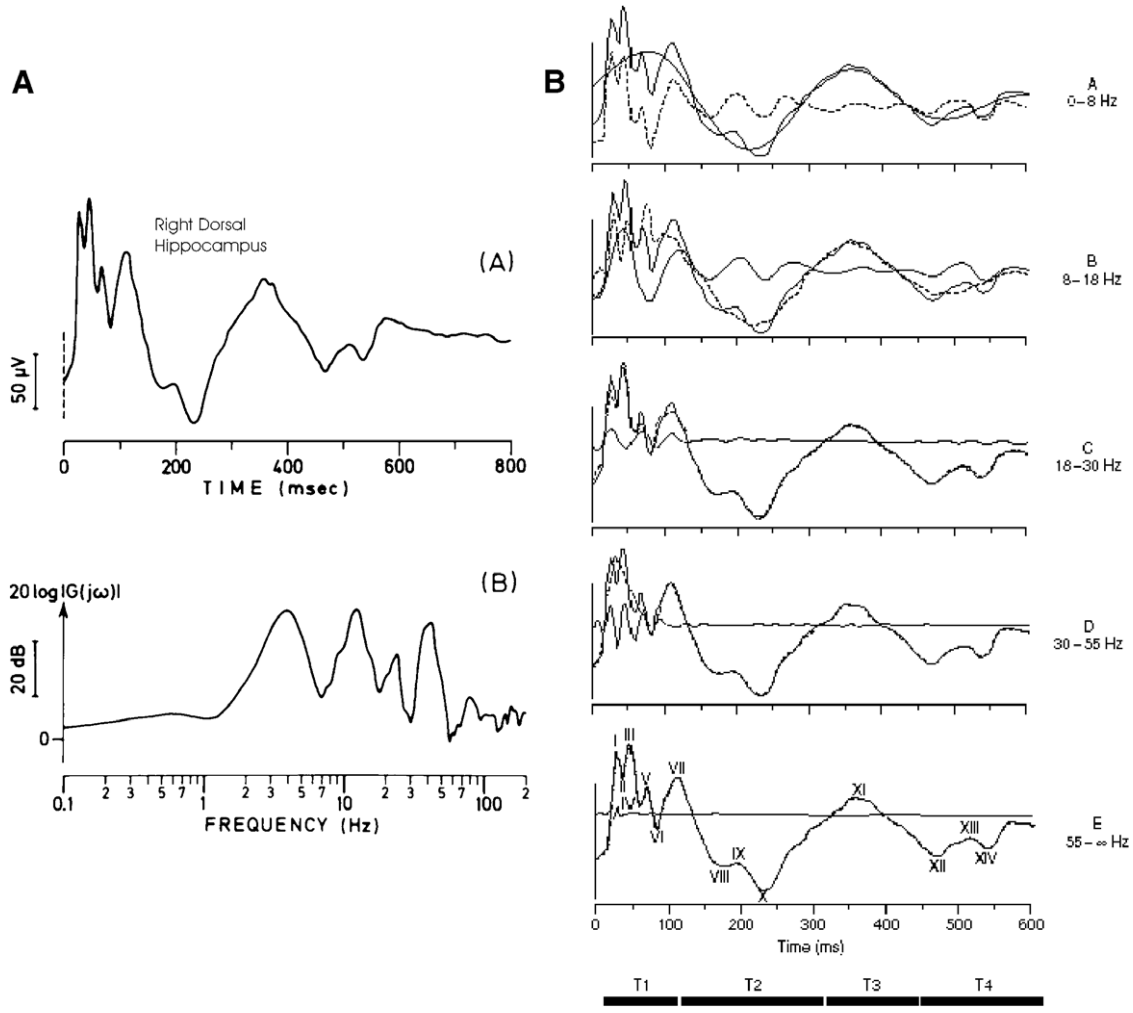

Fig. 1. (A) Averaged EP (A) recorded from the right dorsal hippocampus of the cat after auditory stimulation in the form of a step function (3-s long tone burst at intensity of 2000 Hz), negativity upward. (B) Amplitude frequency characteristics computed from the transient response (A). Double logarithmic presentation along the abscissa-log (frequency) and along the ordinate-relative amplitude in decibels. (Modified from Başar (1980), in *EEG Brain Dynamics: Relation between EEG and Brain-Evoked Potentials*, Elsevier, Amsterdam.). (B) Filtering of a selectively averaged hippocampal EP with different stop- and pass-bands. Solid lines represent filtered averaged EPs obtained with application of pass-band filters. Dashed lines represent filtered averaged EPs obtained with application of stop-band filters. The band limits (at right of averaged EPs) of the applied filters were chosen according to the TRFC method. The original selectively averaged EP is shown for comparison with filtered averaged EPs. Time sections T1 through T4 are shown at the bottom. Note the ample gamma responses with comparable values to alpha response filters. (Modified from Başar (1980), in *EEG Brain Dynamics: Relation between EEG and Brain-Evoked Potentials*, Elsevier, Amsterdam).

averaged ERPs. The filtered curves obtained show the time course of oscillatory activity in a certain frequency range.

3. Remarks on physiology of selectively distributed oscillatory processes

To proceed with the terminology of *physiological memory* and *perceptual memory*, we need the knowledge related to EEG correlates of *sensations, perception, learning and remembering*. Accordingly, at the beginning of this report, we present the processes of activation of alpha, theta, and delta systems with schematical presentations.

3.1. Connections of the sensory–cognitive systems in the brain

Certainly, the connections in the brain are much more complicated as it will be presented in the following, but the chain of ideas and proposals presented in this chapter provide insights to strategies also useful in memory research.

Flohr (1991) describes the anatomical connections in the brain in a simplified and transparent manner as illustrated in Fig. 2.

3.1.1. Specific afferents from sense organs reach specific thalamic nuclei before going to primary cortical areas

For instance, auditory information is transmitted through the medial geniculate nucleus to the primary auditory area; visual afferents are transmitted through the lateral geniculate nucleus to area 17 of the occipital cortex.

3.1.2. Non-specific afferents reach the cortex from the mesencephalic formation

It has now been established that reticular formation is connected to different nuclei with specific afferent connections. There is a second site where the reticular formation influences the processing of primary afferents: the thalamic

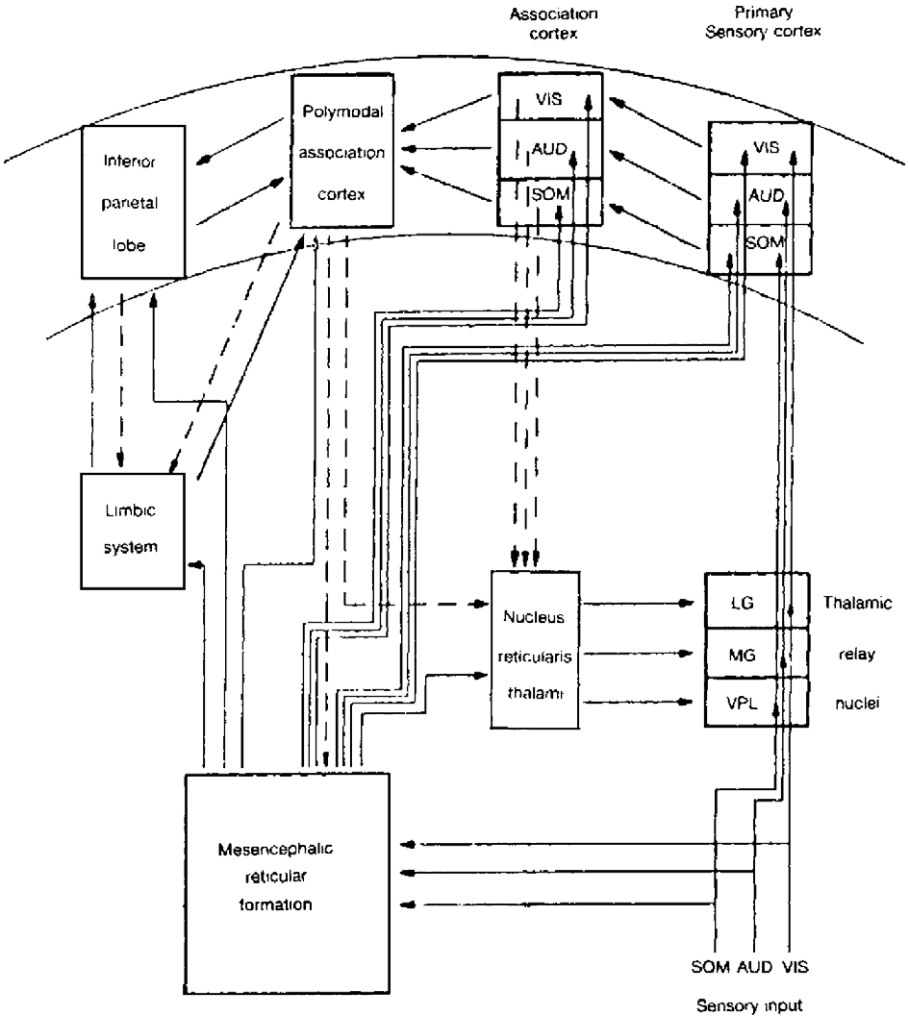

Fig. 2. Flow of information in auditory, somatosensory, and visual pathways, reticular formation, limbic system, and association areas of the cortex. (Modified from Flohr, H., *Theory and Psychology*, 1, 245, 1991).

relay nuclei. The nucleus reticularis thalami, a thin sheet of neurons, surround the dorsal thalamus and inhibit the thalamic relay nuclei. Its control function is, in turn, affected by collaterals of thalamo-cortical pathways, by collaterals from cortico-thalamic projections and by inhibitory afferents from the mesencephalic reticular formation. There are important connections within the cerebral cortex involving the association areas. Primary auditory, somatosensory and visual fields each project to adjacent unimodal association areas, which, in turn, project to secondary unimodal association fields. The unimodal association areas project to a number of polymodal sensory areas, lying in the cingulate gyrus, parietal, temporal and frontal lobe. The functions of these areas are vaguely described as a cross-modal association and synthesis. The polymodal association areas project to the inferior parietal lobe, which has been termed a "*supramodal*" area. Polymodal and supramodal regions have connections to the limbic system; these connections provide the anatomical substrate by which motivational states influence cortical processing of sensory stimuli.

Every sensation in the brain also induces cognitive loading, at least for matching processes. Furthermore, all presented cognitive targets evoke sensations; the respective neural processes are interwoven and require, for final processing, at least three neural loops next to purely sensory connections in the simple sensory systems. These loops are:

1. "*Secondary connections*" to the cortex over reticular formation.
2. "*Secondary connections*" over the limbic system.

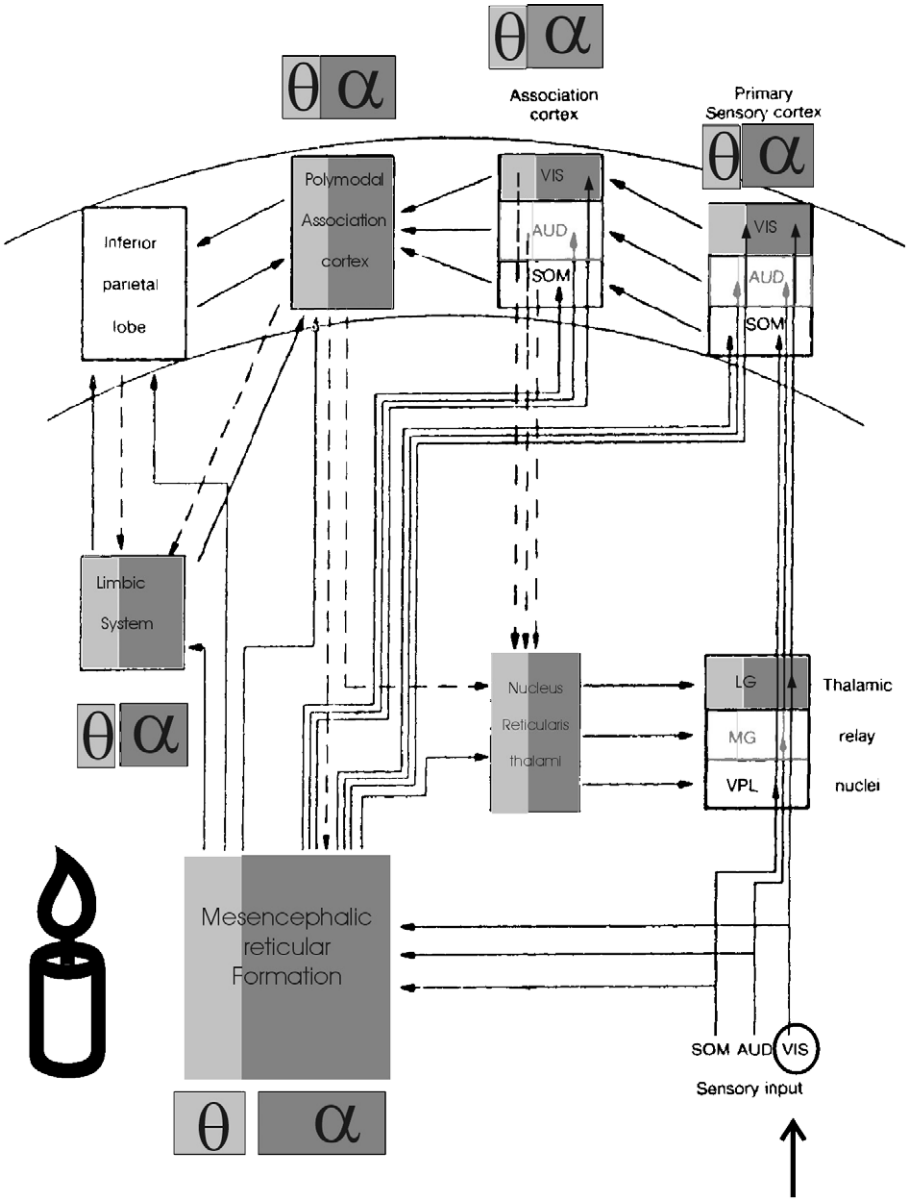

Fig. 3. Flow of oscillatory information in alpha and theta frequency channels in visual pathway, reticular formation, limbic system, and association areas of the cortex. The alpha and theta indicate strong enhancements.

3. "*The connections within the cortex*" between association areas.

3.2. Activation of alpha system with light

When a subject (human or cat) has been visually stimulated, large alpha enhancements are recorded in the mesencephalic reticular formation, lateral geniculate nucleus and, in parallel, in the hippocampus. There are also large alpha enhancements in the visual and association cortices. The information flows to the polymodal association cortex and to the limbic system. Large theta enhancements were recorded in the thalamus, hippocampus, primary cortex, and association cortices including the frontal lobes (Başar, 1999). The same figure illustrates that alpha enhancements cannot be observed in the auditory areas of the cortex and thalamus upon visual stimuli; however, theta enhancements are present in these structures also following light stimulation.

The neurophysiological processes in subcortical structures are explained in Fig. 3. Large alpha and theta enhancements are observed in the limbic system, reticular formation, and lateral geniculate nucleus. No alpha enhancements are recorded in nuclei of the auditory pathways. Although the theta enhancements are one of the major response components also in the thalamus and the cortex, the alpha responses are not recorded in the auditory cortex and the medial geniculate nucleus.

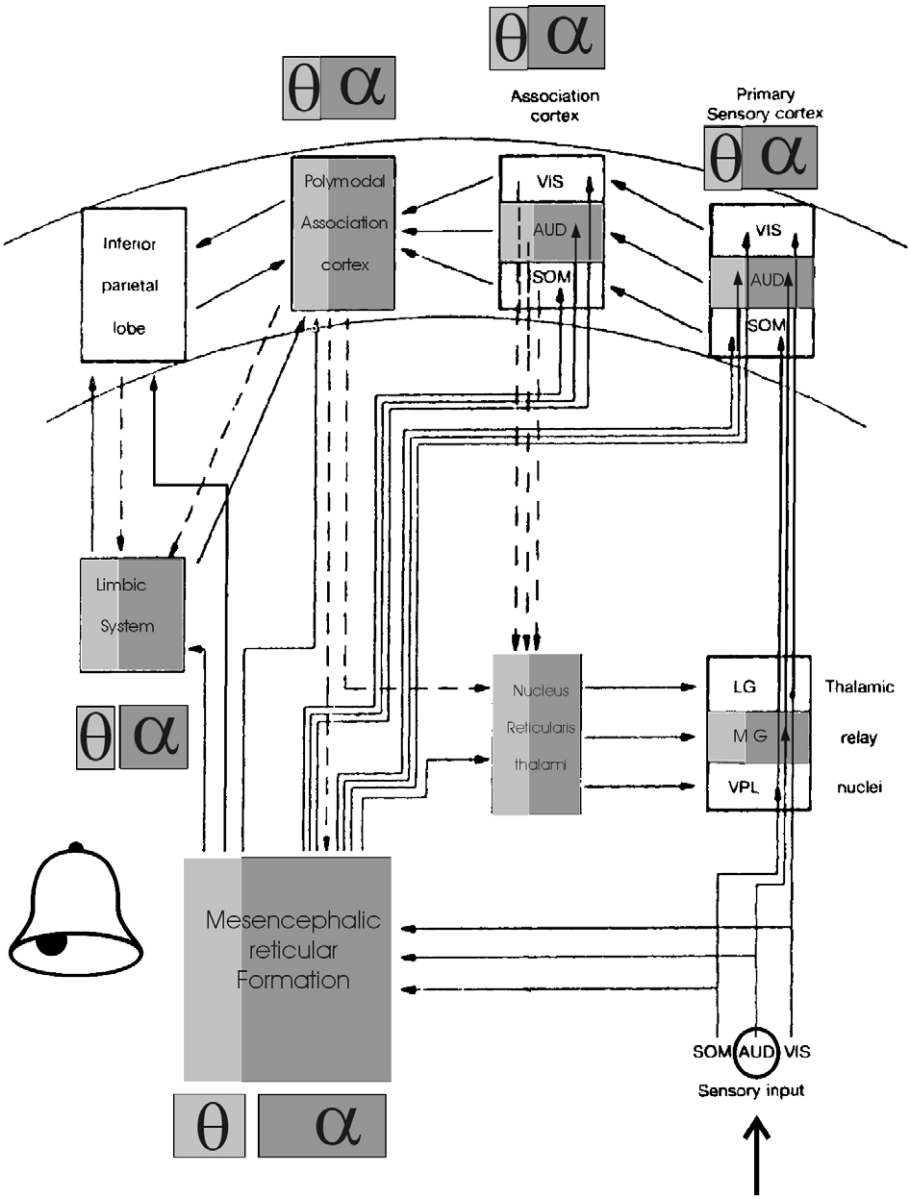

Fig. 4. Flow of oscillatory information in alpha and theta frequency channels in the auditory pathway, reticular formation, limbic system, and association areas of the cortex. The alpha and theta indicate strong enhancements.

3.3. Activation of the alpha system with auditory stimulation

Fig. 4 explains a similar hypothetical flow of information upon an auditory stimulation. In this case, alpha enhancements dominate the structure in the auditory pathways, i.e., reticular formation and hippocampus. The neurophysiological processes in subcortical structures depict large alpha response components in the reticular formation, medial geniculate nucleus, and the auditory cortex. It is noteworthy that the reticular formation and the hippocampus show large alpha responses, whereas the lateral geniculate nucleus and visual cortex only show theta responses. Theta enhancements are present in all structures, regardless of whether the stimulus is adequate or inadequate. The way of thinking used for auditory stimulation can be applied to visual stimulation also, but now the largest alpha enhancements are marked in temporal, parietal and occipital areas.

3.4. Activation of theta and delta systems following cognitive inputs

We again use the same anatomical pictures of Fig. 2 to explain the electrical responses occurring in the region of 300 ms upon application of a cognitive target. For the sake of simplicity, we do not consider the delayed and prolonged 10 Hz responses and take into consideration only the dominance of delta, and theta responses. Experiments described by Başar-Eroğlu et al. (1992) and Başar-Eroğlu and Demiralp (2001) confirmed large delta and theta enhancements around 300 ms following the stimuli. Fig. 5 explains the process limited to approximately 1 s following a cognitive (i.e., target) stimulus.

When the stimulation applied contains an event-related target, the hypothetical flow of information would show large theta, and delta enhancements in all areas of the cortex, but probably also in the substructures. Large theta and delta

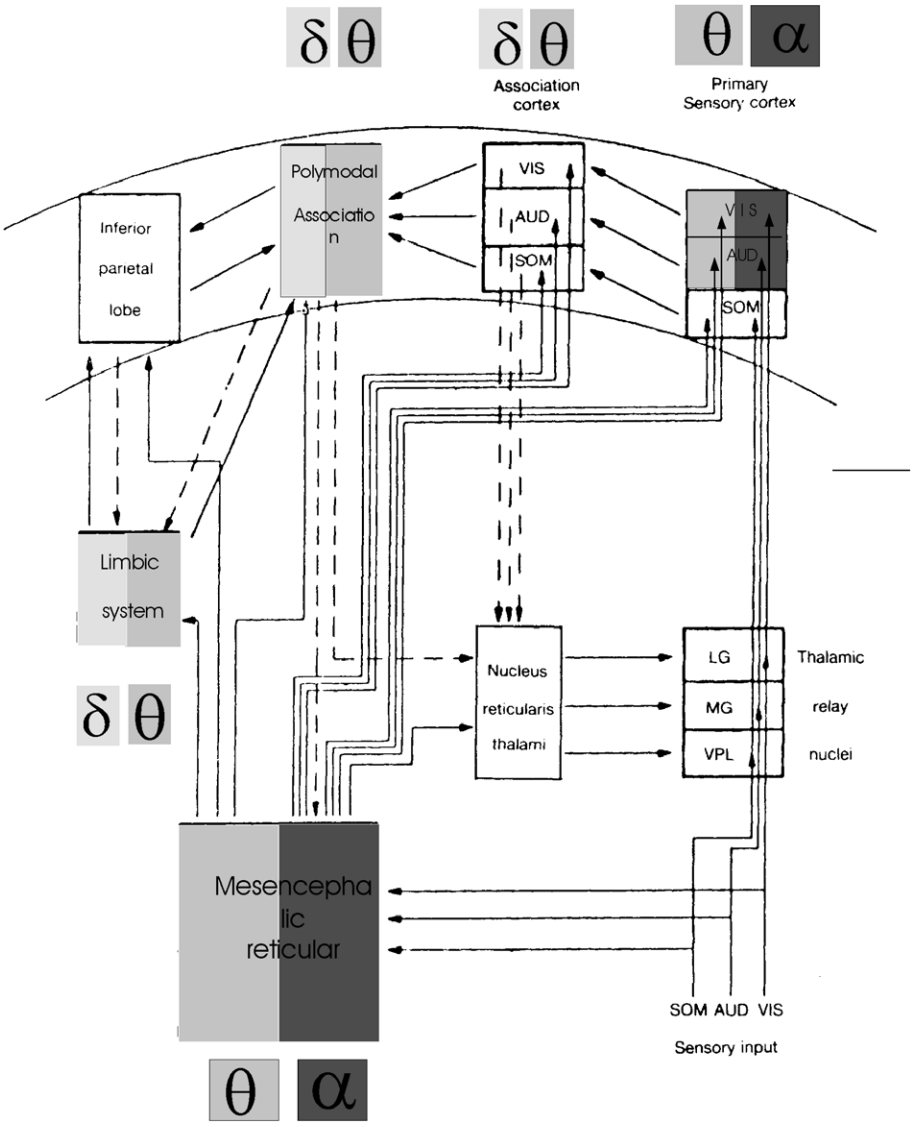

Fig. 5. Flow of oscillatory information in theta and delta frequency channels in the visual (VIS) and auditory (AUD) pathways and limbic system. The theta and delta indicate strong enhancements.

responses and delayed alpha responses would be first observed at 300 ms after stimulation.

3.5. Non-specific interactions

Many animals have quiescent or inattentive states. In vertebrates, a neural system associated with arousal to the attentive state (part of the reticular activating system) receives inputs from many senses. The arousal system influences neurons in almost all brain nuclei that deal with specific sensory information. Thus midbrain, thalamic, and cortical neurons primarily responsive to visual stimuli may be activated or modulated by auditory or somatosensory stimuli via nonspecific arousal mechanisms (see also Chapter 2 in Başar, 1999).

The cross-modality response experiments demonstrate that the differences between responses to adequate stimulation and responses to inadequate stimulation ("adequate/inadequate differences") were marked in the alpha frequency range and less marked in the theta range (see Figs. 3 and 4 above). This hints at a possible special role of the alpha response in primary sensory processing. This means that alpha responses are also correlated with cognitive processes, but the auditory alpha response is not ample in the occipital cortex, accordingly the APLR-related *alpha response* of the occipital lobe is activated during visual processing. Vice versa, in primary auditory areas (temporal lobe) the APLR-related *alpha response* is also activated during visual processing. In contrast, theta responses appear to be less dependent on whether the stimulus is adequate or not, which is compatible with a predominantly associative–cognitive role of the *theta response* as hypothesized above and as published earlier (Başar et al., 1991; Demiralp and Başar, 1992; Başar-Eroğlu et al., 1992; Başar-Eroğlu and Demiralp, 2001).

We repeat here Hartline's statement (1987) about the visual cortex, which is considered to be involved exclusively with vision: In cats, about one-third of the neurons in area 17 (striate cortex), 18, and 19 are reported to be responsive to sound as well as to visual input. Briefly, it was hypothesized that "adequate" stimulation of a cortical area (e.g., visual stimulation/visual cortex) is followed by a response with a high amplitude alpha component and a theta response of small amplitude. "Inadequate" stimulation elicits responses with less difference in the theta and alpha responses, i.e., in the case of inadequate stimulation the theta response is less reduced than the alpha response. In other words, the alpha response appears to be more dependent on the "adequacy" of the stimulus than the theta response.

4. Hierarchical categorization of different levels of memory

4.1. Fuster's view on memory networks

According to Fuster (1995), the cognitive functions of the frontal cortex as any part of the neocortex consist in the activation and processing within and between *networks of representation* or *memory networks*. Those networks are *widely distributed* and *highly specific*, defined by their synaptic structure and connectivity. Thus the memory code is a relational code, and *all memory is associative*. Further, Fuster states that the cortical networks of memory extend across modules and areas by any anatomical definition. To our opinion, one of the most important concepts of this author is the fact that *memory networks overlap* and are *diffusely interconnected* with one another. Thus, one neuron or group of neurons anywhere in the cortex can be part of many networks and thus many memories: this is why it is virtually impossible, by any method, to localize a memory. The networks of executive or motor memory are distributed in the cortex of the frontal lobe and are like the perceptual networks of posterior, post-rolandic cortex hierarchically organized. This statement is in accordance with the described functioning of selectively distributed oscillations that cannot be exactly localized.

4.2. The tentative model related to EEG activation

In all living beings, memory is incorporated into survival functions ranging from the simplest reflex to the higher nervous activity, including episodic and semantic memory processes. Accordingly, the hierarchy of memory functions is categorized at all the levels of living and survival processes. We tentatively introduce *three different levels of memory states* in the scheme of Fig. 6.

At **Level I**, we include *inborn* (built-in memories), i.e., networks that are active during *retrieval processes* that are genetically coded and, are usually not altered, or less altered during life.

At **Level II**, we include dynamic memory states, which are activated and interactive with integrative functions.

At **Level III**, *longer term memory activation* is included. As we will see in the coming sections, no exact boundaries between these levels can be described.

4.3. Inborn (built-in) networks (Level I)

In order to establish a hierarchical classification of inborn memories, we propose three levels of inborn memory, which can be classified as parts of the *physiological (or fundamental–functional memory)*: They are

1. Simple reflexes
2. Complex reflexes
3. Stereotypic fixed action patterns
4. Phyletic memory
5. Feature detectors
6. Living system settings

4.3.1. Reflexes

Memory, learning, and integrative functions in the CNS arise from operations of networks of adaptive elements.

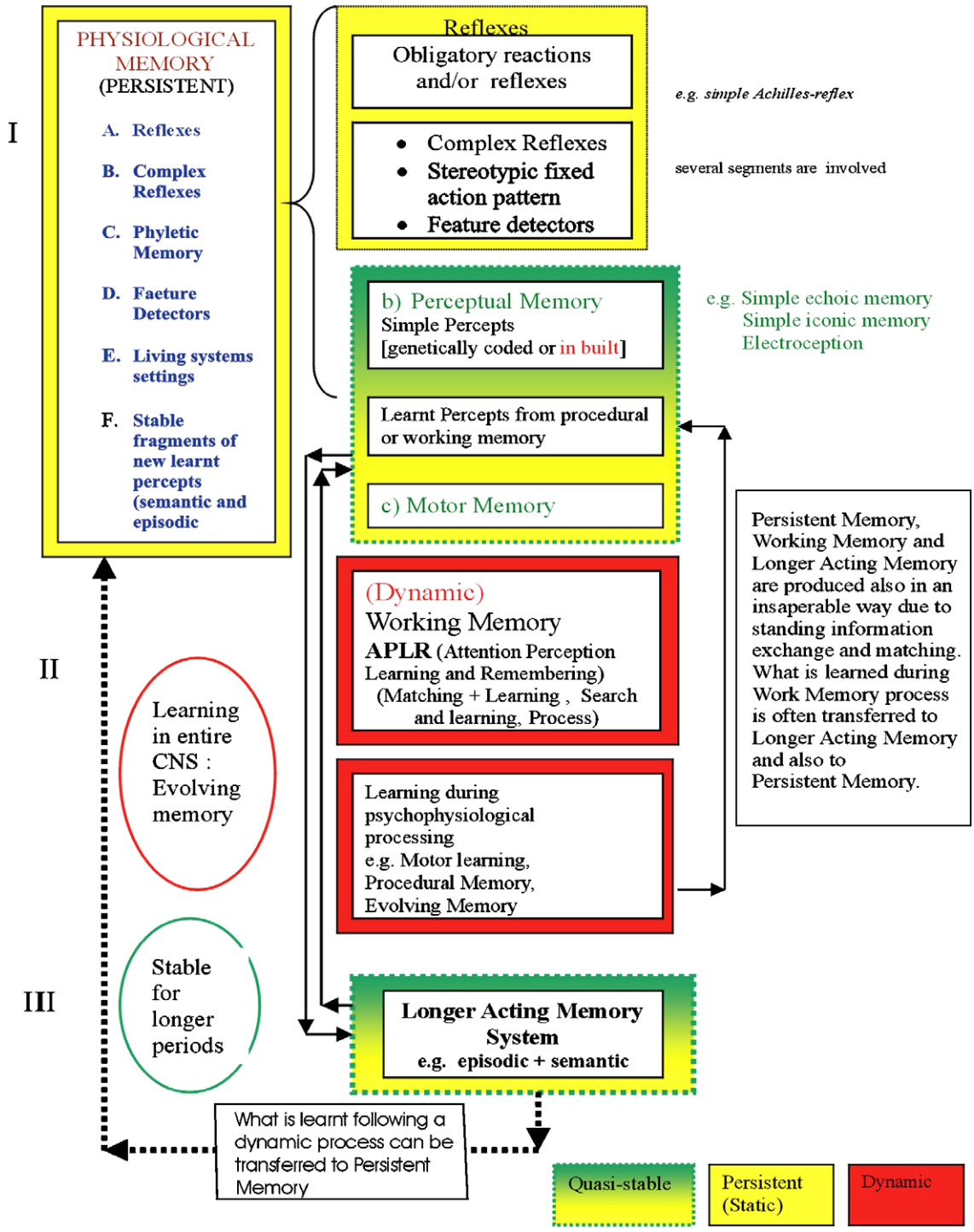
I
PHYSIOLOGICAL MEMORY (PERSISTENT)
A. Reflexes
B. Complex Reflexes
C. Phyletic Memory
D. Faeture Detectors
E. Living systems settings
F. Stable fragments of new learnt percepts (semantic and episodic
Reflexes
Obligatory reactions and/or reflexes
e.g. simple Achilles-reflex
Complex Reflexes
Stereotypic fixed action pattern
Feature detectors
several segments are involved
b) Perceptual Memory
Simple Percepts
[genetically coded or in built]
e.g. Simple echoic memory
Simple iconic memory
Electroception
Learnt Percepts from procedural or working memory
c) Motor Memory
II
(Dynamic)
Working Memory
APLR (Attention Perception Learning and Remembering)
(Matching + Learning , Search and learning, Process)
Persistent Memory, Working Memory and Longer Acting Memory are produced also in an insaperable way due to standing information exchange and matching. What is learned during Work Memory process is often transferred to Longer Acting Memory and also to Persistent Memory.
Learning in entire CNS : Evolving memory
Learning during psychophysiological processing
e.g. Motor learning, Procedural Memory, Evolving Memory
III
Stable for longer periods
Longer Acting Memory System
e.g. episodic + semantic
What is learnt following a dynamic process can be transferred to Persistent Memory
Quasi-stable
Persistent (Static)
Dynamic

Fig. 6. Draft of a detailed scheme of memory levels, hierarchy, and transitions between memories. Level I (top) is persistent memory, of which the essential part is physiological or fundamental memory composed of inborn (or built-in) memories including monosynaptic simple reflexes (e.g., Achilles reflex); complex reflexes involving multiple segments of the spinal cord, stereotypic fixed action patterns (e.g., flight reaction of aplysia); and phyletic (echoic and iconic) memories and electroception ability. Living systems settings such as blood pressure, smooth muscle reaction, and heart beat belong to physiological memory as does motor memory. The yellow background shows static components; such memory types are persistent. The green–yellow background is associated with quasistable longer term memory states. Newly learned percepts acquired after activation of procedural or working memory are quasi-stable and acquired during life. They are not inborn but exist for long periods. Over time, they may be replaced or forgotten. Perceptual memory is between Level I and Level II. Level II covers dynamic processing and the working memory state. Dynamic changes in the APLR alliance are strongly associated with evolving memory. Following motor learning or procedural memory, new engrams can be created and are then transferred to perceptual or motor memory as indicated by an arrow. Following learning during procedural or evolving memory states, newly memorized information is transferred to longer term memory (Level III). Semantic and episodic memories are categorized at this quasi-stable level indicated by gray and yellow. Newly learned material following a dynamic process is sometimes transferred to persistent memory (Level III to Level I) as the arrow indicates.

Physiologically, the elements are neurons and the networks may be considered as reflex pathways *linking inputs* and *outputs* by way of specifiable transforms. There are many reflex systems, some being as simple as those in the spinal cord as described by Sherrington, and others, much more complex. L. P. Pavlov (1927) and B.F. Skinner (1938) gained insights into reflex processes supporting learning and memory in the last century. They appreciated the fundamental significance of the reflex as a mediator of behavior. Sherrington (1948) provided physiological documentation of the neural pathways that connected stimulus with response. It was shown that a knee-jerk elicited by tapping the tendon below the patella is mediated by two types of neurons.

4.3.2. Stereotypic fixed action patterns and phyletic memory

To illustrate this, we can refer to the fixed action pattern of the "escape actions" of *Aplysia californica* when in contact with a starfish. Fuster (1995) states that for the understanding of the formation and topography of memory, it is useful to think of the primary and sensory motor areas of the cortex that we may call *phyletic memory* or *memory of the species*. The structure of primary sensory and motor cortices may be considered a memory deposit that species have acquired through evolution. We can call it memory because, like personal memory, it is the information that has been acquired and stored, which can be retrieved (recalled) by sensory stimuli or by the need to act. In the structure of primary systems, phyletic memory contains the innate capacity to respond to and to recall the elementary features of sensation and movement that are common to the repertoires of all members of the species.

4.3.3. Feature detectors

Primary features of stimuli such as heat, force, light, sound, and chemical substances are selectively transduced at the peripheral ends of sets of sensory (afferent) nerve fibers. Different groups of these sensory fibers respond selectively at lower thresholds than do others, to different forms of impinging energy. This "*tuning*" is often called "*feature detection*" and is accomplished during the evolution of species by the development of specific transducer mechanisms for different forms of energy, either in the nerve endings themselves or in complex sensory organs in which afferent fibers terminate. Examples of these are the mammalian retina, cochlea and the pressure transducers of the primate hand skin (see the statements of Sokolov, 2001, and of Mountcastle, 1998).

4.4. What is physiological memory? What is fundamental memory?

We introduce the physiological memory as the ensemble of memories or living system settings that are necessary for all vital functions: *Physiological memory is a fundamental memory*; and the functioning of the CNS is impossible without this (see Fig. 6). It is genetically coded and differentiated among species. It includes sensory memories such as *echoic* and *iconic* memory; it also includes *reflexes* and *stereotypic action patterns and perceptual memory*.

According to the flow charts in Figs. 3, 4, and 5 sensory and perceptual memory machineries are manifested with multiple oscillations in the alpha, beta, gamma, theta and delta frequency bands.

According to Fuster (1995) there are as many networks as there are memories and, in theory their number is infinite. In all living systems, depending on the level of evolution or the type of species, there are several types of reflexes and also differentiated forms of sensory memory. To make this differentiation understandable we include few examples:

The ray has poor vision. But it has the ability of *electroception.* Lampreys do not see at all and have the ability of electroception. Mammalians do not have the ability of electroception but have well-developed hearing and vision. Reflexes vary from the simplest Achilles reflex to the stereotypical behavior reflexes. All these types of fundamental reflexes belonging to physiological functioning are extremely important for survival. The physiology of electroception of the ray is explained in Chapter 7 in Başar (1999) and also Bullock and Başar (1988).

Recently, we have reviewed several classifications of memories given by distinguished memory investigators to find a strategy to explore the electrophysiology of distributed memories. We concluded that recording of event-related oscillations (EEG and ERPs) could provide a good method to attack the problem both at the neurophysiological and psychological levels since brain oscillations have similar frequency codes in the whole brain (Başar, 1999, Başar et al., 2000). Further, cognitive inputs evoke in the brain oscillatory responses are similar to sensory oscillatory responses both in the same EEG frequency channels. Only, *prolongation, amplitudes and topological distributions* are different.

Accordingly, interactions in sensory–cognitive processing are rich, and separation of these processes is almost impossible. Recall and memory are manifestations of various and multiple functional processes depending on the complexity of the input to the CNS. The electrical response to a simple light flash stimulation forms the bases of simple memory processes at the lowest hierarchical order.

In the schematic illustrations of Figs. 3 and 4, it is seen that sensory cortices and thalamic nuclei do react with alpha response to sensory stimulation. This means that occipital alpha response is an inborn or built-in response for *iconic memory*, reacting to simple light stimulation; vice versa alpha response of the auditory cortex is a built-in physiological response to auditory simple stimulation. Again, the early gamma response is also one of the components of phyletic memory response.

4.5. Living system settings incorporated in physiological memory

4.5.1. Sympathetic system and EEG oscillations

Living system settings are ensembles of detectors and all types of mechanisms that serve living systems to maintain survival functions such as normative values of blood pressure, respiratory rhythms, cardiac pacemakers, and body temperature. Such mechanisms that are important to maintain the body within the limits of healthy life qualities should be also categorized into the level of persistent memory since damage to these settings strongly affects higher levels of nervous activity and all levels of memory activation. Gebber et al. (1995) reviewed a series of articles from their laboratory on the 10-Hz rhythmic sympathetic nerve discharges of cats and offered a hypothesis on its functional significance.

The rhythm is ubiquitous to the discharges of sympathetic nerves with different cardiovascular targets and arises from a system of coupled nonlinear brain stem oscillators, each of which has a selective relationship with a different portion of the spinal sympathetic outflow. The 10-Hz rhythmic discharges of sets of sympathetic nerves are differentially related and the pattern of relationships in one experiment can be the reverse of that in the next. The authors hypothesize that non-uniform and dynamic coupling of the central circuits controlling different sympathetic nerves is the basis for the formulation of complex cardiovascular response patterns that include differential changes in regional blood flow.

Are there tuning and matching effects between cognitive 10-Hz oscillations and sympathetic discharges? This question may be answered in the future. However, the fundamental findings of Gebber's group indicate that the physiological settings of the circulatory system and of phyletic memory characteristics are in the 10-Hz frequency range. A link between cognitive and vegetative processes may possibly be supplied with general 10-Hz oscillations.

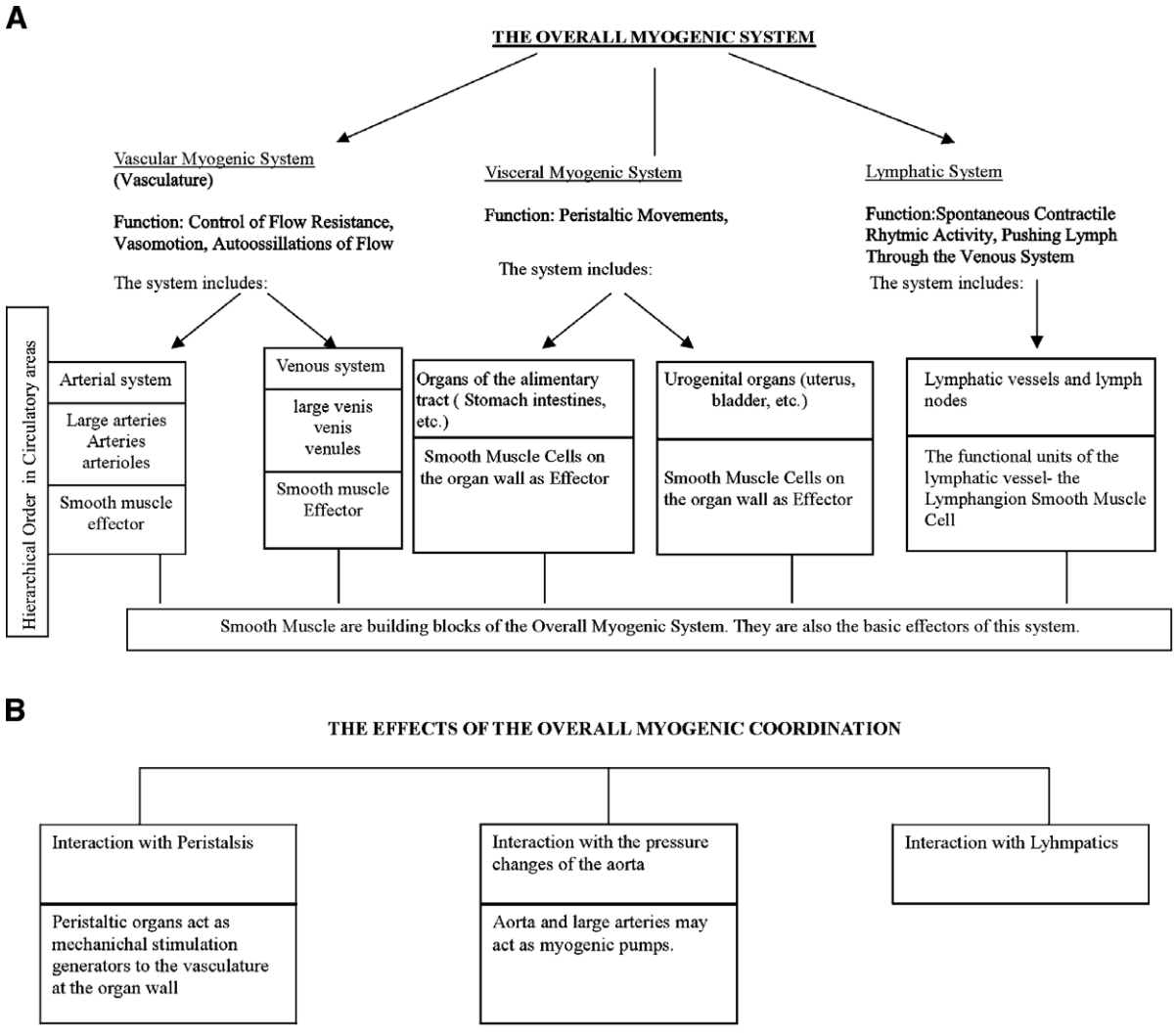
A
THE OVERALL MYOGENIC SYSTEM
Vascular Myogenic System
(Vasculature)
Function: Control of Flow Resistance, Vasomotion, Autoossillations of Flow
The system includes:
Visceral Myogenic System
Function: Peristaltic Movements,
The system includes:
Lymphatic System
Function:Spontaneous Contractile Rhytmic Activity, Pushing Lymph Through the Venous System
The system includes:
Hierarchical Order in Circulatory areas
Arterial system
Large arteries Arteries arterioles
Smooth muscle effector
Venous system
large venis venis venules
Smooth muscle Effector
Organs of the alimentary tract (Stomach intestines, etc.)
Smooth Muscle Cells on the organ wall as Effector
Urogenital organs (uterus, bladder, etc.)
Smooth Muscle Cells on the organ wall as Effector
Lymphatic vessels and lymph nodes
The functional units of the lymphatic vessel- the Lymphangion Smooth Muscle Cell
Smooth Muscle are building blocks of the Overall Myogenic System. They are also the basic effectors of this system.
B
THE EFFECTS OF THE OVERALL MYOGENIC COORDINATION
Interaction with Peristalsis
Peristaltic organs act as mechanichal stimulation generators to the vasculature at the organ wall
Interaction with the pressure changes of the aorta
Aorta and large arteries may act as myogenic pumps.
Interaction with Lyhmpatics

Fig. 7. (A) Schematical presentation of the overall myogenic system. (B) Schematical presentation of the effects of the overall myogenic coordination.

Başar and Weiss (1981) measured and reviewed mechanisms of control, auto-oscillations of blood flow, contractility of the vasculature, forced oscillations in the peripheral circulatory system, spectral activity of peristaltic organs, dynamics of the lymph nodes and the lymphatic system and found that all these subsystems showed spectral properties (oscillatory activity) in the ultra-slow frequency range of 0.01 Hz, 0.04–06 Hz and 0.1 Hz. This author introduced the concept of the "overall myogenic system" after quantifying and treating the performance of smooth muscle dynamics, by considering this as the dynamics of an overall and coordinated dynamic system. The overall myogenic system incorporates:

(1) The "*vascular system*," with all the arteries, arterioles etc. in the systemic circulation.
(2) The "*lymphatic system*" with lymphatic vessels and nodes.
(3) The "*visceral system*," which performs the visceral functions of the vegetative system and peristalsis in vegetative function.
(4) The smooth muscle cells are building blocks and basic effectors of the overall myogenic system (see Fig. 7A showing the organization of the overall myogenic system and Fig. 7B schematically describing the effects of overall myogenic control). According to the measurements of Başar (1981), the "overall myogenic coordination " occurs in the common frequency ranges of 0.01, 0.04–0.05 and 01 Hz, thus corresponding or overlapping with the frequency range of new measurements of in the literature (Allers et al., 2002).
(5) Aladjalova (1957) demonstrated ultra-slow periodicities in the brain as early as 1957. There are in the meantime a number of publications indicating the existence of these ultraslow oscillations and the possible links with the EEG (Ruskin et al., 1999). Multi-second oscillations in firing rate with periods in the range of 2–60 s (mean, 20–35 s) are present in 50–90% of spike trains from basal ganglia neurons recorded from locally anesthetized, immobilized rats. To determine whether these periodic oscillations are associated with similar periodicities in cortical activity, transcortical electroencephalographic (EEG) activity was recorded in conjunction with single- or dual-unit neuronal activity in the subthalamic nucleus or the globus pallidus, and the data were analyzed with spectral and wavelet analyses (Allers et al., 2002). Multi-second oscillations in firing rates of 31% of the STN neurons and 46% of the GP neurons with periodicities significantly correlated with bursts of theta (4–7 Hz) activity in transcortical EEG.

These are concrete examples showing the possibility of ultra slow wave oscillatory coordination between myogenic organs and the brain.

4.6. Genetic factors are fundamental in living system settings and physiological memory

The group of Begleiter and Porjesz launched recently a fundamental approach to examine the genetic underpinnings of the neural oscillations. It is proposed that the genetic underpinnings of these oscillations are likely to stem from regulatory genes which control the neurochemical processes of the brain, and therefore influence neural function (Begleiter and Porjezs, in press). According to the publications of this group, genetic analysis of human brain oscillations may identify genetic loci underlying the functional organization of human neuroelectric activity and brain oscillations represent important correlates of human information processing and cognition. Further, these oscillations represent highly heritable traits that are less complex and more proximal to gene function than either diagnostic labels or traditional cognitive measures. Therefore, these oscillations may be utilized as phenotypes of cognition, as well as valuable tools for the understanding of some complex genetic disorders (Begleiter and Porjesz, in press). Genetic loci that have been recently identified regarding both resting and evoked brain oscillations involving the GABAergic and cholinergic neurotransmitter systems of the brain are discussed by these authors (see also Kamarajan et al., 2004; Porjesz and Begleiter, 1996, 2003; Porjesz et al., 1998, 2002).

The advent of genomics and proteomics and a fuller understanding of gene regulation will open new horizons on the critical electrical events so essential for human brain function.

Since the oscillatory system settings have fundamental role in memory, the genetic settings belong also to the Level I of the memory model of Fig. 6,. Accordingly, the genetic factors will be possibly incorporated in phyletic memory and physiological memory in our model in the next evaluations.

4.6.1. Change of sensory memory during life. Spontaneous and evoked alpha activity at occipital sites in three age groups

The visual cortex needs visual experience during a critical period of early life in order to achieve its full functional development. In the absence of critical experience, the cortex remains defective. As a consequence of this, normal vision cannot be attained or the subject would need considerable training.

There are in the literature vast amount of results indicating the change of oscillatory responses after acquiring new experiences. The example in Fig. 8 explains that after learning and training in the early period of life, the alpha activity and alpha responsiveness do change. In the earlier period of life, there are no alpha responses to simple light stimulation and accordingly, the functioning of networks sensitive to light and sound (Başar, 1998) are susceptible for changes. The phyletic memory and the

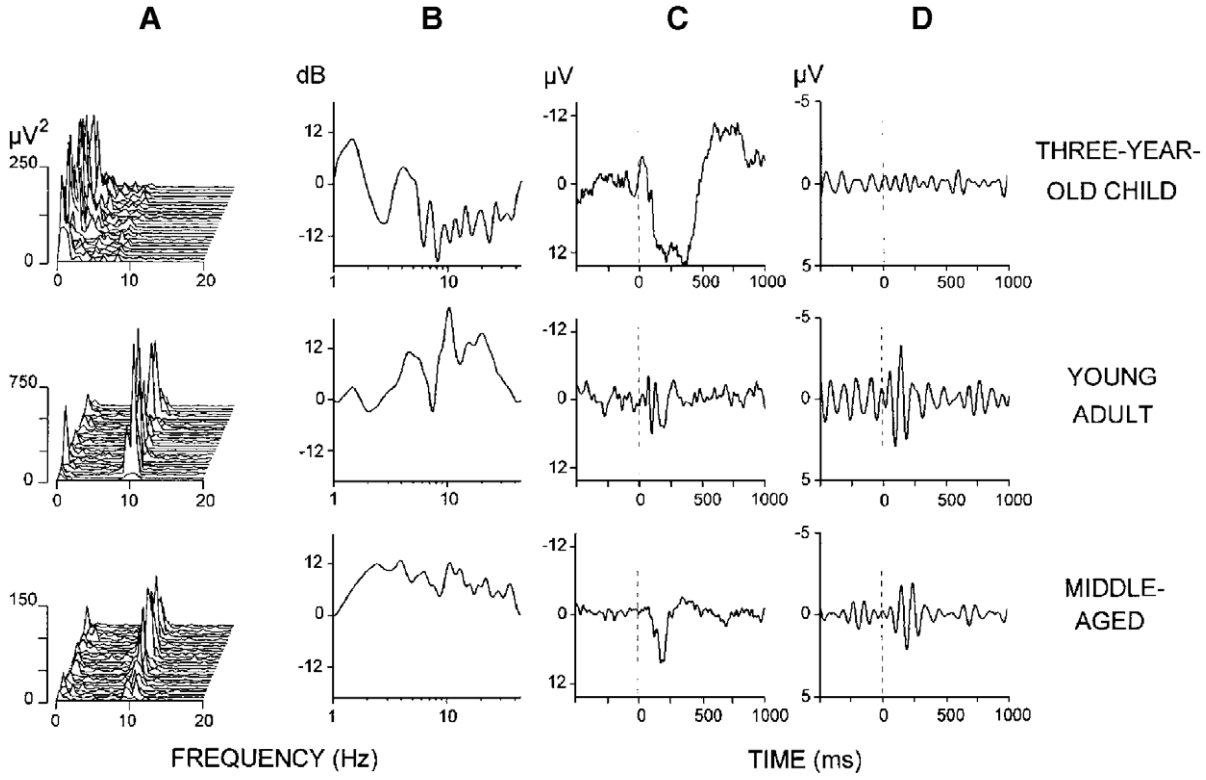

Fig. 8. (A) Instantaneous power spectra of consecutive 2-s long EEG epochs. (B) Amplitude frequency characteristics of visual-evoked potentials (VEPs). (C) Averaged VEPs. (D) VEPs filtered in the range of 8 to 15 Hz. Subjects were a 3-year-old child, young adult, and middle-aged adult. All recordings are from the left occipital site O1. Stimulus onset occurred at 0 ms. (From Başar et al. (1997c), *Int. J. Psychophysiol*., 26, 1).

physiological memory are not perfectly stable during lifetime.

During a memory process–either a shorter or longer term one–the perception of a sensory input is *matched* with information already stored in the neural tissue. When a simple light evokes alpha and gamma responses in the cortex, elementary oscillatory responses are also strongly associated with several memory processes at different hierarchical levels. The topology of the memories depending on the modality of the input must be different (see examples given above: cross-modality experiments; measurements in cortical and subcortical structures). During a perception process, the brain performs a *matching process* with inborn sensory memories. Even complex percepts are interwoven with simple sensations. Since processing of simple sensations and complex percepts are inseparable, the physiological memory and perceptual memory must also be inseparable; they rather built an entity. We propose the existence of an *alliance of physiological and perceptual memories*. This consideration has a crucial consequence: Although in the schema of Fig. 6 physiological and perceptual memories are presented separately, they *overlap* in the functional processing.

According to these facts, physiological and perceptual memories do not depict a clear-cut functional hierarchy or absolute separation: The illustration should, in reality, show a *continuum between physiological and perceptual memory*. It should not present an absolute functional hierarchy or separation. This statement is in accordance with the described functioning of selectively distributed oscillations (see also Fuster's statement in the foregoing Section 4.1).

By discussing the elements of the schematical presentation of Fig. 7, we will find out that it is quite impossible to define most of memory types or levels as fully separated individual entities with rigid (frozen) boundaries in the time and topological spaces as in the case of perceptual memories. On the contrary, learnt reflexes and simplest sensory cognitive processes and all types of memories have dynamic features, *they are steadily evolving as life continues*. Following a learning process, our semantic memory is already altered or extended.

So far, such studies demonstrating these dynamical processes have rarely been performed; the experiments on the recognition of grandmother face belong to this type of experiments (Başar et al., 2004; Özgören and Başar, 2003) Therefore, results and their interpretations have to be considered as preliminary and rough steps. Accordingly, the multiple distributed memories cannot be treated in detail and a perfect classification on all levels of distributed memories cannot be yet provided. Probably, such classifications can never be perfectly reached. Therefore, the model of in Fig. 6 presents a proposal incorporating the dynamic memory and evolving memory.

4.7. Working memory, dynamic memory (Level II)

During processing of many complex tasks, it is necessary to hold information in temporary storage to complete the task. The system used for this is referred to as *working memory* (Baddeley, 1996). Working memory is the temporary, ad hoc; activation of an extensive network of short- or long-term perceptual component of that network would be, as any other perceptual memory, retrievable and expandable by a new stimulus or experience. Fuster (1995) states that working memory has the same cortical substrate as the kind of short-term memory traditionally considered as the gateway to long-term memory.

The detection of a target signal during a P300 type of experiment requires also a type of working memory. The subject has to sustain knowledge related to the target (nature of the target, frequency, shape, color etc., depending on the type of the experiment) during the experiment. The linkage between P300 amplitude and latency measures and working memory processes has been already established (Sanquist et al., 1980; Howard and Polich, 1985; Pratt et al., 1989; Fabiani et al., 1990; Scheffers and Johnson, 1994). The matching process after the detection of the target should rely in this case on working memory or the success of this type of memory P300 versus N100. In Chapters 3, 4 and 6 of Başar (2004), it is shown that during working memory and evolving memory states alpha, delta and gamma oscillations are differentially activated.

4.8. Perceptual memory

Several types of analysis categories are crucial in the functional interpretation of ERPs.

The analysis of the stimulus itself: What can a stimulus evoke in the brain? It can evoke simple percepts, complex sensory percepts, bimodal percepts or memory related functions, etc.

According to Fuster (1995 p. 10), *perceptual memory* is memory acquired through the senses. It comprises all that is commonly understood as personal memory and knowledge, i.e., the representation of events, objects, persons, animals, facts, names and concepts. Fuster further describes that in the hierarchy of memories, at the bottom originally acquired by sensory experience, have become independent from it in cognitive operations. This means that perceptual memory partly belongs to *built-in* memory types, and during life it evolves by adding new stored percepts and becomes richer in stored information. Therefore, perceptual memory comprises elements of phyletic memory of fundamental memory and also elements of semantic and episodic memories. Here, again, it is not possible to define exact boundaries in the hierarchies of perceptual, semantic and episodic memories. In order to process percepts, the brain does not only need the built-in networks of elementary sensations but also new ones obtained information during life. We include *perceptual memory* also to category of *quasi-stable* memories in the

Notes to Table 1:

The term theory may be used to signify any hypothesis whether confirmed or not, or may be restricted to hypotheses that have been strongly confirmed as to become part of the accepted doctrine of a particular science. In its best use, it signifies a systematic account of some field of study, derived from a set of general propositions. These propositions may be taken as postulates, as in pure mathematics, or they may be principles more or less strongly confirmed by experiences, as in natural science. (From Encyclopedia Britannica.)

The NeuronsBrain Theory describes a systematical account of measurements on electrical activity of neural assemblies, and it also incorporates proposals derived immediately from measurements. Accordingly, in Table 1, we underline some principles on electrical activity of neural assemblies that are derived from measurements.

1) The Brain has natural frequencies or oscillations measurable at the cellular and population levels.
2) Brain oscillatory responses are real responses related to function (Başar et al., 2001a,b,c,d).
3) Oscillations are selectively distributed and selectively coherent.
4) Oscillations are related to multiple functions and a given function is often manifested by means of multiple oscillations (Klimesch, 1999, 2000). Principle of superposition is confirmed by several publications (Karakaş et al., 2000a,b).

A natural consequence of the NeuronsBrain Theory (or Brain Assemblies Theory) is the super-synergy in oscillatory dynamics. The proposition or a model for the electrical manifestation of the grandmother percept is based on evident facts: Research shows that the increasing complexity of percepts is accompanied with increased number of multiple oscillations in parallel with increased number of activated neural populations. Although the proposal related to the perception of the grandmother is a fictive one, it is anchored on tenable arguments: Could the grandmother percept involve multiple and distributed oscillations instead of the firing of a unique cell (Stryker, 1989)? A semi-empirical approach to the explanation of the grandmother percept would be through the concept of super-synergy. According to results described in the present previous reviews selectively distributed and selectively coherent oscillatory networks in the delta, theta, alpha, beta and gamma bands play a major role in brain functioning. Sensory and cognitive events evoke superimposed multiple oscillations that are transferred to spatially distributed tissues almost in parallel with various degrees of amplitude, latency, duration, synchronization and coherence. Sakowitz et al. (2001) reported significant gamma response amplitude increases in distributed areas of the brain and a 100% frontal theta enhancement by bimodal stimulation compared to unimodal one. It was (Başar et al., 1993) reported that retrieval of visual experience from short-term memory is associated with 40 Hz activity. The coherences between different spatial locations of the brain vary as these areas are activated with different classes of stimuli (haptic and visual) in an associative learning task (Başar, 1988). Such findings experimentally substantiate the submechanisms that have been outlined above. Accordingly, we suggest that complex percepts (such as the visual image of one's grandmother) are formed and/or manifested by means of the ensemble of oscillatory superbinding dynamics.

The complex memory function (episodic and semantic memory) is placed in the column adjacent to the proposal to Grandmother or to Perception of Gestalt. This arrangement of the table is in accordance with the references indicating the increasing number of involved populations and frequency windows with the increased complexity at the functional level.

illustration of Fig. 6. Because, according to the descriptions above, the perceptual memory is *partly inborn*, however complex percepts acquired during life are often not completely stabilized, they are quasi-stable. (For example, the grandmother percept is shaped by several events during life and is not an inborn percept Başar et al., 2004). In Sections 2, 3 and 4, it was shown that alpha, gamma and theta responses responding to simple light or simple sounds are generated probably from built-in networks, since cross-modality experiments demonstrate that alpha sensory response is evoked only by adequate stimuli in cortex and thalamus (Section 3.5). The perceptual memory is distributed not only in primary areas of the cortex and thalamus, but also in the whole brain since alpha responses were recorded in the whole brain (see Figs. 3 and 4).

According to the considerations above, we classify the simple perceptual memory also as part of physiological memory. However, recognition of complex percepts that show individual differences is less linked to the ensemble of physiological memory. The recognition of complex percepts is more overlapping or interwoven with the ensembles of

Table 1
Principles derived from measurements and related to electrical activities of neural assemblies

Priciples of neuro-electricity *(measured)*	Functional level	Examples *(measured)*	Activated memory (*Tentative hierarchy*)	Some references
1. Brain shows oscillary neural activity a. Oscillations are almost invariant in evolution b. Oscillatory respnses are real brain responses	Very simple functions or Functional building blocks ↓ Integrative neurophysiology and Cognition ↓ Very complex functios	• α-response • γ-response (components of auditory and visual responses • δ-response at the visual and hearing threshold	• Phyletic memory • Simple sensory memory • Decision making	Başar, (1992) Başar et al. (2000) Başar & Schürmann, (1994) Demiralp et al. (1999) Gruzelier et al. (1996) Karakas and Başar (1998)
2. a. Each oscillatory activity represents multiple funtions vice versa b. Each function is represented by multiple oscillations *Superposition principle*		• Frontal θ, occipital α • Oddball • P300: Superposition of δθαγ responses • α-expectation	1. Encoding association 2. Working memory 3. Decision making 4. Upgrading memory 5. Dynamic memory	Başar, (1999) Başar et al. (1987) Başar and Stampfer, (1985) Başar-Eroğlu et al. (1987) Karakas et al. (2000) Klimesch, (1999) Maltseva et al. (2000)
3. Multiple oscillation are selectively distributued in the brain as parallel processing			Memory is selectively distributed	Başar et al. (1975, 2000) Courtney et al. (1997) Fuster, (1995, 1997) Goldman-Rakic, (1997) Gruzelier, (1996)
4. Selectively distributed parallel oscillatory systems are integrated in function Various topology dependent enhancements phase locking, delays, prolongations, in parallel processing		PROPOSAL e.g. perception grandmother GESTALT	Episodic ↓↑ Semantic memory	Basar et al. (2000) Burgess, (2002) Doppelmayer, (2002) Klimesch, (1999, 2000)
Increasing number of neural populations		Increasing complexity at the functional level	Increasing memory complexity	

subsets of *evolving memory*. The processes of recognition and of evolving memory are dynamic processes that are manifested by multiple oscillations.

A reason for mentioning working memory in the current section is due to the fact that this memory function has been linked to the prefrontal region of the brain, i.e., part of the dorsolateral frontal lobe that comprises the anterior convexity of the cerebral hemispheres (Goldman-Rakic and Friedman, 1991; Fuster, 1991). However, most of the studies of working memory have been done in non-human primates, making it difficult to draw direct neuroanatomical comparisons to humans. Nonetheless, there is strong evidence in non-human primates that the prefrontal region plays a crucial role in working memory, and it is likely that this relationship will, at least to some extent, apply to humans as well (see Baddeley, 1986a,b, Chapter 10 in Başar, 2004).

4.9. Incorporation of oscillatory codes in physiological memory consisting of phyletic, sensory and perceptual memory

In the Fig. 6, we have tentatively presented that the physiological memory incorporates phyletic, sensory and perceptual memories. Do these memory types or activated memory states are interwoven with similar frequency codes?

Several publications show that the mammalian brain responds to simple visual and auditory stimuli with selectively distributed alpha, theta, beta, gamma and delta responses (see Table 1 and Figs. 3 and 4 above).

As we explained in earlier publications (reviewed by Başar, 1999) alpha, theta and gamma responses are also manifestations of phyletic memory, since they are inborn and possibly wired responses. This fact is clearly indicated in the fourth column of the Table 1, which describes the hierarchy of activated memories.

According to the results by Başar et al. and flow charts in Figs. 3, 4 and 5, sensory and perceptual memory machineries are manifested with multiple oscillations in the alpha, beta, gamma, theta and delta frequency bands.

Our empirical evaluation suggests that all these memory types are interwoven and/or tuned with the frequency codes of the EEG oscillations. This fact can facilitate the transition between memory states and communication. Besides this, strong links or alliance with all integrative functions in the brain could be rapid progressed.

4.10. What is motor memory and procedural memory development during life?

According to Fuster (1995), *motor memory* consists of representations of motor action in all its forms, from skeletal movement to spoken language. Motor memory, like perceptual memory, is evoked and acquired through the senses, but once acquired; it is largely presented in the neocortex and frontal lobe. The most automatic and firmly established aspects of motor memory are represented outside of the neocortex: basal ganglia and the cerebellum are most fundamental structures related to motor memory. Perception and motor action are interrelated, and both are part of many representational networks.

According to Baddeley (1986a,b), procedural memory refers to the acquisition of skills, whether perceptual-motor, such as those of riding a bicycle or driving a car, or cognitive, such as in skilled reading or problem solving. They clearly comprise an important area of learning and do of course represent the archetypal example of procedural learning—*learning how* rather than *learning that.* Baddeley describes that skills can be divided into two types: *continuous*, in which each component of the skill serves as a cue to the next, as in cycling or steering a car; and *discontinuous*, in which a series of discrete stimulus–response links are involved, as in typing. In general, continuous skills seem to show little or no forgetting, whereas forgetting clearly occurs with discontinuous tasks.

Specifically, the basal ganglia have been linked to various forms of non-declarative memory, particularly those types of memory that are dependent upon a motor act for their realization, or what has been termed *procedural memory* (e.g., riding a bicycle, skating). The cerebellum, another motor-related structure situated behind the brainstem at the base of the brain, participates along with the basal ganglia in many types of procedural learning and memory (e.g., Glickstein, 1993; Thompson, 1986, 1990, see also Chapter 4 in Başar, 2004). In the illustration of Fig. 6, *perceptual* memory and *procedural* memory are in the category of quasi-stable memories. There are also changes of oscillatory response activity during aging, as it was described in Fig. 8.

5. Dynamic memory in whole brain: “memory states instead of memories”

5.1. Alpha, theta and delta oscillatory processes during APLR

Processes of *Attention, Perception, Learning and Remembering* (APLR) are simultaneous and interwoven (this fact is described in details at the level of EEG oscillations in chapters by Başar, 2004, by Baddeley (1996) and Desimone (1996) at the single cellular level). Fig. 6 shows that the evolving memory is accompanied by the dynamic shaping of theta oscillations in a P300 type of experiment. The interplay between delta and theta activities is completely changed at the end of the experiments. We also mention the dynamic shaping of the alpha oscillations during learning—and dynamic memory experiments were clearly shown in by Başar et al. (1997a,b). Hayek (1952) presents his concept of cortical memory network in the context of the main topic, which is not memory itself, but significantly, perception as

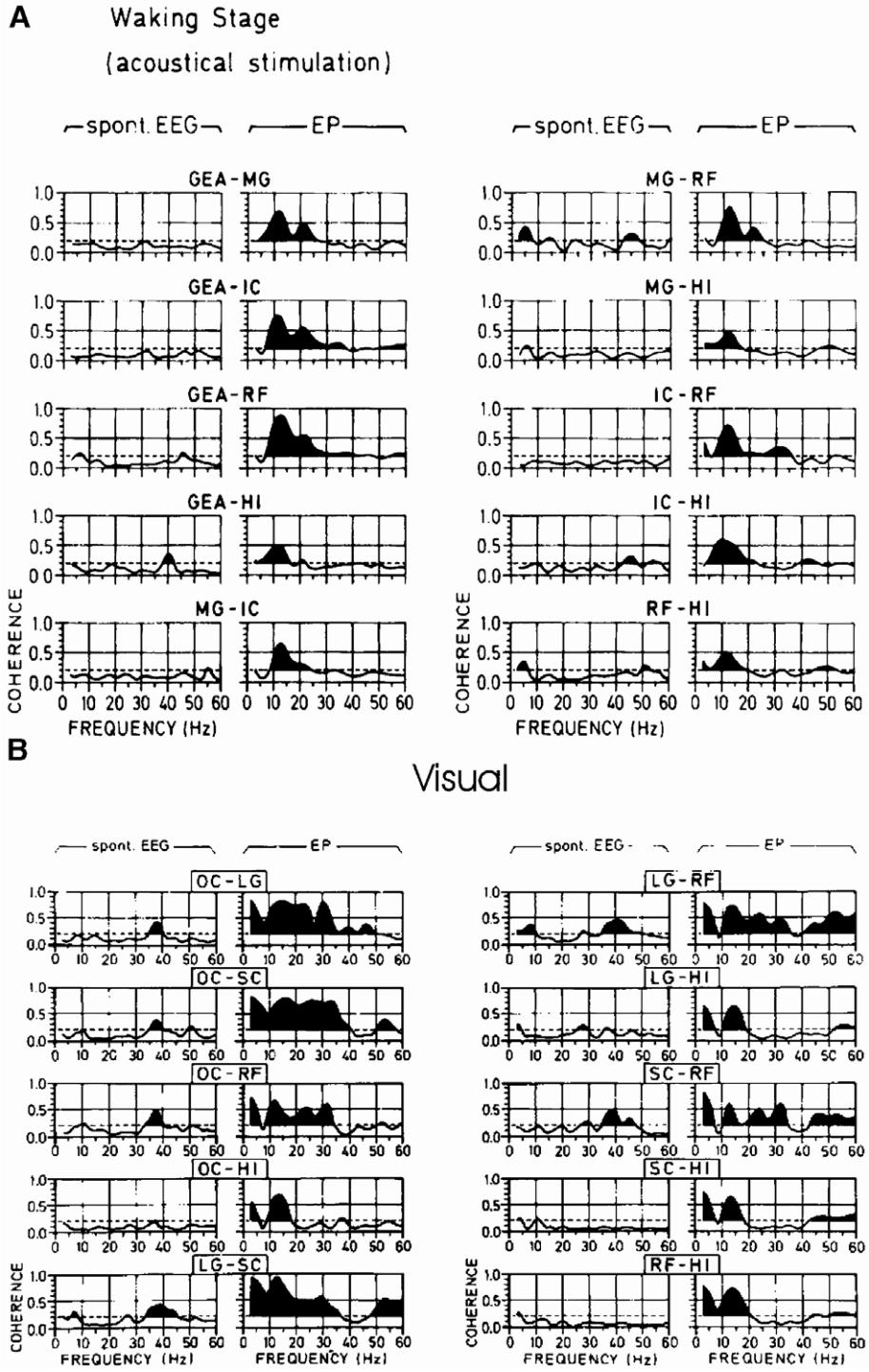

Fig. 9. (A) Typical set of coherence functions computed from the spontaneous activities and EPs of all possible pairings of the studied brain structures during waking (scale indicated at bottom). Along the abscissa is the frequency from 0 to 60 Hz; along the ordinate is the coherence between 0 and 1. The horizontal broken lines indicate significance level (0.2 for all plots). The area under the coherence function is darkened only if the curve surpasses this level. To facilitate a comparison of coherence values computed from spontaneous and evoked parts of the EEG-EP studies, the respective coherence functions are presented as couples for all pairings of recording electrodes. (From Başar (1980), in *EEG Brain Dynamics: Relation between EEG and Brain-Evoked Potentials,* Elsevier, Amsterdam.). (B) Typical set of coherence functions computed from spontaneous activities and visual-evoked potentials of all possible pairings of studied brain structures (scale indicated at bottom). Along the abscissa is the frequency from 0 to 60 Hz; along the ordinate is the coherency between 0 and 1. The horizontal broken lines indicate significance level (0.2 for all plots). The area under the coherence function is darkened only if the curve surpasses this level. To facilitate a comparison of coherence values computed from spontaneous and evoked parts of the EEG-EP studies, the respective coherence functions are presented as couples for all pairings of recording electrodes. (Modified from Başar et al. (1979a), *Biological Cybernetics*, 34, 2130).

the *source* of memory and as the *product* of memory. We introduced APLR alliance as a consequence of the measurements: It is not a theoretical construct, but it is derived from the empirical evidence.

5.2. Are dynamic EEG templates created during processing of the alliance of APLR? Do such templates build a (virtual) short-term storage of the new learned material?

During learning tasks, the oscillatory activity does change when subjects acquire new knowledge.[1] These changes are manifested by newly created EEG templates (Fig. 6). Further, such changes are probably consequences of matching processes and are at least *temporarily stored* in the brain. As a metaphor it can be stated that, (1) during processes of working memory oscillatory components do also work, often in a superimposed way, and that (2) the oscillations "work" in parallel in the whole brain as coherence analysis has indicated. Fig. 9A and B illustrate that alpha and theta long-distance coherences are increased upon presentations of auditory and visual stimuli in the cat brain. These evoked coherences are selectively distributed in the whole brain depending on the stimulation modality.

Attention, perception, learning and memory do work in synergy and in a reciprocally activating and interwoven way as also the coherency data demonstrated.

Further, this description, which is experimentally founded, indicates that *attention, perception, learning, and dynamic memory* are inseparable functions representing an entity, rather then presenting separable processes. In processing of complex functions, the *brain waves work longer*, have multiple components, and accordingly, during complex signal processing *delay* or *prolongation* of the oscillatory activities are observed. Difficulty to recognize a target in the oddball paradigm or in the omitted sound paradigm is manifested by delay and prolongation (Karakaş et al., 2000a,b).

5.3. Are all functions of the brain linked with memory?

According to Goldman-Rakic (1996)[2], working memory is the ability to hold an item of information transiently in mind in the service of comprehension, thinking and planning. Working memory encompasses both storage and processing functions. It serves as a *workspace* for holding items of information in mind as they are recalled, manipulated, and/or associated to other ideas and incoming information.

In earlier publications, we have shown that during experiments with cognitive loadings, the oscillatory prestimulus and post-stimulus activities reflect *constant work of the brain in progress*: Alpha activity prior to expected cognitive targets goes to a state of order, the time course of the alpha activity is ordered, aligned, amplitudes of oscillations are increased during cognitive demands and memory loads. Further, the alpha oscillations are phase locked to the expected target signal (Başar et al., 1989, 1997a,b; Barry et al., 2003a,b). If we bring these results together with the statement of Goldman-Rakic (1996), we come to our main scope by considering all brain functions and memory as an entity: Possibly we should better talk about " *Memory and Brain Functions Alliance*" as a more general categorization of APLR alliance. We should better say that all brain functions are memory linked or all memory is function.

As an example, the qualitative and quantitative properties of the alpha activity are changing and *evolving* during experimental sessions, thus giving the message that alpha activity is involved with *constant work*. This work reflects parallel and reverberating multiple components: *attention, perception, learning and remembering are interrelated and interwoven*.

The memory types like *procedural memory, working memory, motor learning* have been categorized at the ***Level II*** of Fig. 6. Motor memory is more difficult to be categorized solely on one level, it is to be categorized between Levels I and II.

6. Complex or "multiple matching" evolving memory, and the APLR alliance

Pribram (1963) defines the memory as any set of events that makes available to an organism something of a situation after that situation no longer obtains. By the term "thought," Pribram refers to the active uncertainty produced when an ordered set of memories **mismatches** the current novelties of the situation. According to Fuster (1995), neural memory is special in several ways among them is its capacity not only to retain information but also to utilize it for adaptive purposes. In this sense, neural memory becomes connatural with learning, from which it is operationally difficult to distinguish it, although the term learning usually refers to the process of acquiring memory. The schematic illustration of Fig. 6 also takes into account the processes explained in the statements by Fuster (1995) and Pribram (1963): according to our experimental work, we extended the concepts of Hayek and Fuster, with the inseparability of perception and memory and by proposing that processes of attention, perception, learning and memory are difficult to distinguish, and that they are interwoven and inseparable.

[1] "*Learnable sequences*" are time intervals in which stimuli alternated in some predictable order, produced smaller P300 responses than irregular sequences, which were unfamiliar and unpredictable. The findings of studies of Başar and Stampfer (1985) and those of Donchin et al. (1973) suggest that feed forward from memory can influence the P300 amplitude. If memory correctly predicts the input, the P300 response is reduced: if not, a mismatch is registered and a large P300 wave develops.

[2] Regional and cellular fractionation of working memory, *Proc. Natl. Acad. Sic, Vol93.pp.13473–13480, Nov 96, Colloquium Paper*).

von Helmholtz (1866/1962) introduced the notion of "mental constructs" that are thought to be generated by past experience and to be stored and recalled from memory. Accordingly, percepts are thought to be produced by the comparison of recalled and evoked neural images. What is going on in the brain when such images are evoked? Do these images also evoke electrical potentials in parallel to recalling?

Mountcastle (1998) goes a step further "Perhaps, what we perceive are patterns of neural activity recalled from the memory for the matching *operation*, rather than the activity evoked directly by sensory stimuli themselves?" It will come as no surprise that direct neurophysiological evidence for the processes of unconscious inference has been hard to come. These sets of propositions are included as assumptions to several of the major unsolved problems of neuroscience: how are experiences stored in and recalled from memory; how are neural populations *matched* and *compared*; how does the chosen match flow through the conscious experience, and so on. Nevertheless, the idea of unconscious experience and *matching identification* remains themes of some later psychological theories of perception (MacKay, 1970).

What is happening in every day cognitive process such as recognizing a familiar object? The basic idea here is that after a sensory code is established, the information in *longer term memory* or persistent memory is accessed which is needed to identify the perceived object. If *the matching process* yields a positive result, the object is recognized. This, in turn, leads to the creation of a short-term memory (STM) code. In this case, bottom up pathways are activated which are similar or identical to those, which would serve to retrieve information from LTM (See Klimesch, 1999).

It is also evident that during a process of evolving memory, the *APLR alliance* under goes a complex *multiple matching process*, which develops with the following steps:

(1) What will be learned has to be *matched* (compared) with the stored percepts (or events) of earlier experience.
(2) In a new sequence, attention will be paid to *new learnt percepts,* and
(3) In the ensuing matching process, these percepts will be (re-) matched with new sensory–cognitive inputs.

We also have to say this: If the brain is able to match a coming input with the just *newly learned experience*, *at least temporarily created EEG traces* are needed. Without temporary traces, recurrent inputs during an oddball experiment cannot be compared with already learned material.

Fuster (1997) describes that components of perceptual memory are retrievable and expandable by a new stimulus or experience. Working memory is presumably the same cortical substrate as the kind of short-term memory traditionally considered the gateway to long-term memory. In the description of Fuster a crucial remark is the following: "*Hierarchical organization, however, does not imply that the various individual memories are rigidly stocked and stored in separate cortical domains. Rather, different types of memories – for example episodic, semantic or procedural – are probably interlinked in mixed networks that span different levels of perceptual and motor hierarchies*."

6.1. Multiple and complex matching processes: reciprocal activation of alpha, delta, theta and gamma circuits in the whole brain

6.1.1. Reentry?

"According to Damassio (1997), memory depends on several brain systems working in concert across many levels of neural organization. Memory is a constant work in progress." If this is so, what type of processing should occur at the EEG-level during this constant work in progress? In order to elucidate the role of EEG-related memory, we propose the existence of complex, recurrent (or reverberating) mechanisms. These proposed mechanisms are experimentally founded with results of perpetual changes of alpha, theta delta, gamma and beta oscillations and their dynamical superposition.

The temporarily created templates provide seemingly a dynamic (storage) copy to be compared with new input signals. Further new sensory input to the brain is matched with oscillatory networks including memory traces of phyletic memory and of the memory acquired during life. We have to emphasize also that response oscillations strongly depend on the state of the prestimulus oscillations during working memory processes (see Rahn and Başar, 1993a,b and Barry et al., 2003a,b).

According to Tononi et al. (1992), the notion of *reentry* extends concepts such as simple feedback, feedforward, or recurrent circuits. Reentry is *inherently parallel*, has a statistical nature, and has a distributed nature meaning that it can occur simultaneously within and across several different areas via multiple parallel and reciprocal connections (as seen in cortico-cortical, cortico-thalamic, and thalamo-cortical radiations); it can occur also via more complex arrangements linking the cortex with the hippocampus or with the basal ganglia.

Başar and Stampfer (1985) and Başar (1988) have mentioned the possibility of such recurrent and reentrant neural populations by means of recording of EEG oscillations without using the expression "reentry" (Edelman, 1978, 1987). The gross electrical activity of a neural population selected to fire (to be activated) shows a high degree of variability and plasticity. During the experiments with cognitive load and memory activation, the EEG prior to stimulation was altered, this giving rise, in turn, to new types of responses, since the ERPs are controlled by the EEG activity preceding the stimulation (Başar et al., 1998; Rahn and Başar, 1993a,b: Barry et al., 2003a,b). According to Barry et al. (2003a,b), stimulation creates states of preference. It is noteworthy to emphasize that the control of the prestimulus activity upon responsiveness or excitability has complex behavior. The alpha, delta, theta activities that

create preference-states depend on the modality of sensory–cognitive input and also on the site of the cortex (more references to this topic can be found in Başar et al., 1998, Barry et al., 2003a,b). The selectively distributed oscillations in the cortex, thalamus, hippocampus and various areas of the brain stem were demonstrated by Başar et al. (1975a,b,c) in the cat brain. These authors used a different terminology at that time: "Synchronized selectivity in the whole brain." Accordingly, it can be hypothesized that, during sensory–cognitive processing the oscillatory networks at different levels of the brain are activated as *recurrent or reentrant* circuits. This behavior can be measured during various types of exogenous or endogenous stimuli as the plasticity and evolving behavior of oscillatory prestimulus or post-stimulus activity in the experiments described by Başar and Stampfer (1985). Possibly, the reentrant signals play an essential role to create "*learnable sequences*, as enhancement, alignment of oscillations, as their transition to *preferred phase angles prior expected stimuli* show.

In the Fig. 6, the loops indicate also this recurrent behavior. We also have to say that measurements of EEG oscillations provide the only possibility to check the existence of reentrant circuits in evolving memory and related types of behavior. The following issue is also important: Başar (1980, 1998) and Başar et al. (1997c) have demonstrated that if a brain structure shows spontaneous oscillatory activity, then this structure is susceptible to react or is responsive in the same frequency channel of spontaneous oscillations (Principle of Brain response susceptibility[3], first indicated by Sato, 1963; Sato et al., 1971, 1977).

6.2. Prolonged oscillations, delays and coherent states during complex matching in the whole brain

In Section 3, results of experiments on selectively distributed oscillatory alpha and theta networks in the whole brain were explained by means of schematic illustrations. Sensory cognitive inputs activate not only in the cortex, but also in the whole brain alpha, theta or gamma oscillations, as serial and more heavily parallel processing (see also Başar, 1999). Accordingly, *reciprocal activation of oscillatory networks* and *complex matching* take place in the whole brain. We tentatively extend, therefore, the definition of active memory stated by Fuster (1995) by using the term "*whole brain instead of whole cortex* " as follows: "At any given time in the awake organism, a widely distributed and changing representational network is active in the whole brain. The activation in the whole brain during memory processes has been clearly explained by Başar, 2004, Chapter 4. That is the *active memory manifested by the EEG oscillations*." The extent and topography of active memory are determined by several factors: (1) the present or recent sensory inputs (2) the neuronal ensembles that by association are activated by those inputs and (3) the EEG oscillatory activity prevalent at the time. As the coherence results of Fig. 9A and B show, the widely distributed networks are largely activated in parallel.

We denoted this processes as "*selectively distributed increases of coherence*." In Table 1, we have included the differentiated activation of memory in several hierarchical process. Fuster underlies that (1) *working memory*, which has also been called *operant memory*, is an operant concept of active memory and also (2) that active memory is a state rather than a system of memory. The dynamic changes in the APLR alliance are manifested by the activity of selectively distributed networks in the brain. Networks are innumerable; they are selectively activated upon input to the CNS. The constant dynamic interaction between attention, perception, learning and remembering are represented by selective multiple oscillations and long-distance coherence in various frequency channels (references) that take place upon sensory cognitive stimulation and /or during experiments related to the *APLR alliance*.

By novelty or incertitude of the sensory–cognitive input the number of mismatches is certainly increased, since *new percepts* are not reflected in earlier oscillatory templates, but in the "*newly stored*" oscillatory templates. Therefore, for all brain structures, *it takes time* to match it and the process of remembering has longer time duration. Since every morning I see my secretary, it is no problem to remember her name and who she is; on the contrary, when I have to remember the name of a person who I have not seen for years, the process of remembering needs more time. We have demonstrated that the oscillatory activities, in alpha, gamma, theta and delta do reflect the "*work of the brain*." In cases of novelty or incertitude, our brain works with "delays or prolonged behavior" and needs more time (or it works longer). Parallel to these delays and prolongations in brain's work, we observe "*delays*" or "*prolongation of oscillations*" (see also Özgören et al., 2005).

P300 oscillatory responses (superposition of oscillatory responses) in alpha, theta, and gamma have longer duration, whereas the EPs upon simple sensory input have shorter and damped oscillatory responses (second theta window, alpha prolongation by difficult tasks, delta-delay in P300). The response susceptibility of a brain structure

[3] The response susceptibility of a brain structure depends mostly on its own intrinsic rhythmic activity (Başar, 1980; 1983a,b; 1992; Narici et al., 1990). A brain system could react to external or internal stimuli producing those rhythms or frequency components, which have already been present in its intrinsic (natural) or spontaneous activity, i.e., if in a given frequency range the spontaneous brain rhythms are missing, they will be absent in the evoked rhythmicities and vice versa. The concept of response susceptibility is strongly connected with the rule of excitement states of neuronal populations as suggested by BaşBaşar (1980, 1983a,b, 1992). According to this rule, if a neuronal population is able to produce spontaneous activity in a given frequency range, then this structural group can be brought to a state of excitement in the same frequency range by sensory stimuli. This means that excitability is related to spontaneity. As an immediate consequence, common features of response susceptibility of brain structures are related to general common tuning and generalized resonances in various structures of the brain in alpha, theta, delta, beta and gamma frequency bands.

depends mostly on its own intrinsic rhythmic activity (Başar, 1980, 1983a,b, 1992; Narici et al., 1990). A brain system could react to external or internal stimuli producing those rhythms or frequency components, which have already been present in its intrinsic (natural) or spontaneous activity, i.e., if in a given frequency range the spontaneous brain rhythms are missing, they will be absent in the event-related oscillations, and vice versa. P300-40 Hz, gamma prolongation by difficult memory tasks (Section 3.1 of Chapter 4 in Başar, 2004). In a similar way, when incertitude is decreased and the matching does not require longer duration the oscillations are shorter as shown by Başar-Eroğlu et al. (2002).

When the whole brain is involved in the remembering process, or in dynamic *reciprocal acting*[4] of APLR alliance, *reverberation* of signals between brain structures upon sensory stimulation is most probable. Therefore, the process of matching takes longer. There are probably cross-talks or reverberations between different structures.

Relevant increases of coherence of theta and alpha responses in the whole brain between cortex, brain stem, hippocampus and thalamus were recorded upon sensory–cognitive inputs to the brain (Başar, 1999; Başar et al., 1998). Since the signal at each electrode location mostly reflects the network activity under the electrode, the coherence between two electrodes should measure interactions between two neural populations. In cases of superbinding of all frequencies, we have to see relevant increase of overall coherence, and this is the case, as experimental results demonstrate (Başar et al., 1979a,b; Başar, 1990).

A hypothetical scheme to describe the complex matching is illustrated in the following section.

7. Complex matching

7.1. Matching of multiple oscillations in the whole-brain

In the foregoing sections, we explained the notion of "matching" mentioning the first steps by Helmholtz, followed with the critical statements of Mountcastle (1998) and of Klimesch (1999). In the following, we hypothesize that the matching processes take place by means of superposition (parallel processing) and of serial processing between different brain areas. Further, we assume that the information flow uses multiple frequency codes that are those of EEG oscillations. Resonance phenomena show that various brain structures – including long distant structures – are tuned with the same frequency codes, and that upon endogenous or exogenous stimulations, links or coherences are enhanced within multiple frequency windows: This means that almost all brain areas are tuned to be activated or resonate with the EEG frequency codes (Başar, 1999; Başar et al., 1999a,b,c). Therefore, we are on solid ground to hypothesize multiple-frequency codes for matching processes. This fact once established we do not include the possibility of other matching codes, for example, the process of activation of feature detectors by simple impulse stimulation.

A preliminary hypothetical scheme to describe the complex matching and flow of oscillation-coded information is presented in Fig. 10A. For the sake of simplicity, only *alpha-code* (red), *theta-code* (green) and *gamma-code* (blue) are represented here. For a more complete description, *delta-code, beta code (and additionally alpha1 and alpha2 codes)* should be also inserted into the illustration.

This illustration has been modified again from the schema of Fig. 2, which roughly describes the information flow in the CNS.

It is important to note that the frequency-coded information flow occurs as

(1) *Serial processing* and
(2) *Parallel processing.*

The "*matching processing*" means the following: the inborn alpha, theta, gamma networks facilitate the adequate information flow in these given frequency channels. The received information is matched in all networks in order to evaluate, whether the signals coming from peripheral organs are adjusted or tuned with the alpha, theta, gamma, delta and beta frequency codes. Here "*a simple-matching*" is the comparison with a unique frequency code, for example, the "alpha matching." In the proposed *complex-matching* procedure, comparisons or matching with all frequency codes (alpha, beta, gamma and theta) are fully or partly activated as parallel or serial processing, depending on the nature of performed integrative functions. Since the oscillatory networks are selectively distributed, the participation of individual frequency codes has varying degrees of amplitudes. Once an ample alpha signal has been brought to "*ignition*," all structures can be excited by giving rise to a huge *reciprocal alpha resonance*. By high load of exogenous or endogenous sensory–cognitive input to the brain, a great "*resonance*" can occur in the brain (for resonance phenomena in the brain, see Başar, 1980, 1999).

In case of serial processing, "*delays*" can occur usually in the range of 500 ms, which is maximal time interval needed for information of flow from one structure to another (see Libet, 1991; Miller, 1991; Başar, 1999). The alpha, theta, gamma signals can also circulate between diverse structures when the inputs–endogenous or exogenous ones–contain difficult or complicated information to process, and accordingly *multiple matching* of circulating of all frequency-coded signals with a great number of brain structures in the whole brain is needed. This may be the cause of prolonged oscillations and of the late alpha, theta or gamma windows around 300–500 ms. In this case, evidently, *the whole brain works longer*. We also should

[4] One could describe this also as "*mutual effect*."

emphasize that serial and parallel processing may occur in all levels together in a reciprocal activating manner.

Fig. 10B hypothetically illustrates the multiple matching processes during oddball tasks or tasks requiring working memory or other cognitive tasks. As the experiments by Başar-Eroğlu et al. (1992) and Karakaş et al. (2000a,b) have shown, the ERPs and prestimulus EEG segments are dominated by delta and theta oscillations in P300 responses. Accordingly, in Fig. 10B, thick lines theta (green) and very thick lines delta (yellow) information processing have been

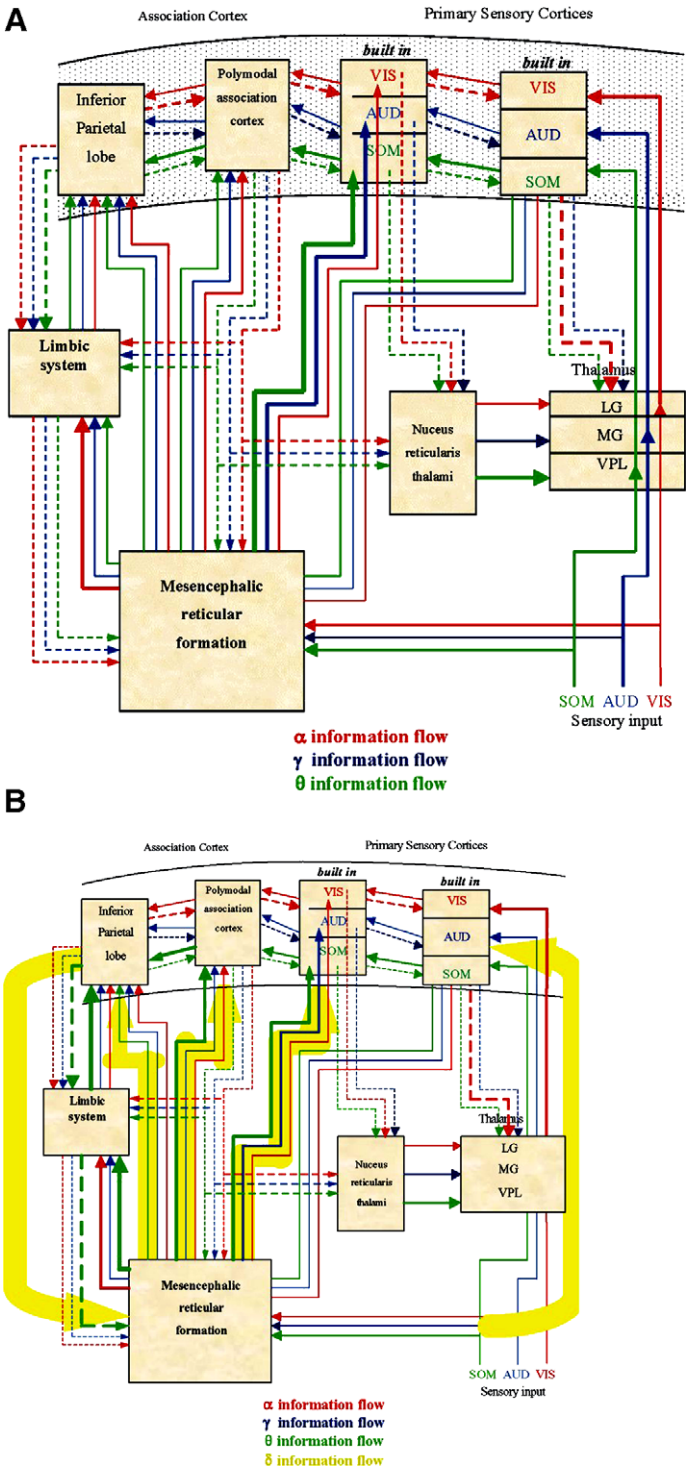

Fig. 10. (A) Preliminary hypothetical scheme to describe complex matching and flow of oscillation-coded information. Alpha code is shown in red; theta in green; and gamma in blue. (B) Preliminary hypothetical scheme of complex matching and flow of oscillation-coded information. Alpha code is shown in red; theta in green; and gamma in blue. Thick lines were added to show dominance of theta (green) and delta (yellow) resonance.

added in order to show the dominance of theta and delta resonance.

We also mention a recent framework proposed by Herrmann et al. (2004) that relates gamma oscillations to two underlying processes: the comparison of memory contents with stimulus-related information and the utilization of signals derived from this comparison. This model attempts to explain early gamma-band responses in terms of the match between bottom-up and top-down information.

8. "Longer acting memory" and transition to "persistent memory" in the whole brain

8.1. Evolving memory is identified as multiple-level functioning in CNS

We introduced the expression "*evolving memory*" or "*memory building*" as activation of memory states or processes, augmented with new learned (memorized) episodes created by *constant and reciprocally active APLR alliance*. The evolving memory includes also the interplay in APLR operations that are manifested as selectively distributed oscillations in the whole brain. We have seen that the oscillatory theta or alpha response related to cognitive inputs do evolve during the APLR process. As an example of the augmentation of knowledge, or the learnt material in CNS, we mention the occurrence of regular and increased alpha activities or types of alpha-templates as demonstrated in Fig. 11.

8.1.1. Level III in activities portrayed in Fig. 6

This level of the scheme of memory hierarchies describes memory states that are categorized at the Level III of the illustration, in Fig. 6.

According to descriptions above, event-related changes in oscillations provide relevant changes and extensions in the electrical manifestations of evolving memory. In this case, it is clear that the *new learnt material* is transformed to

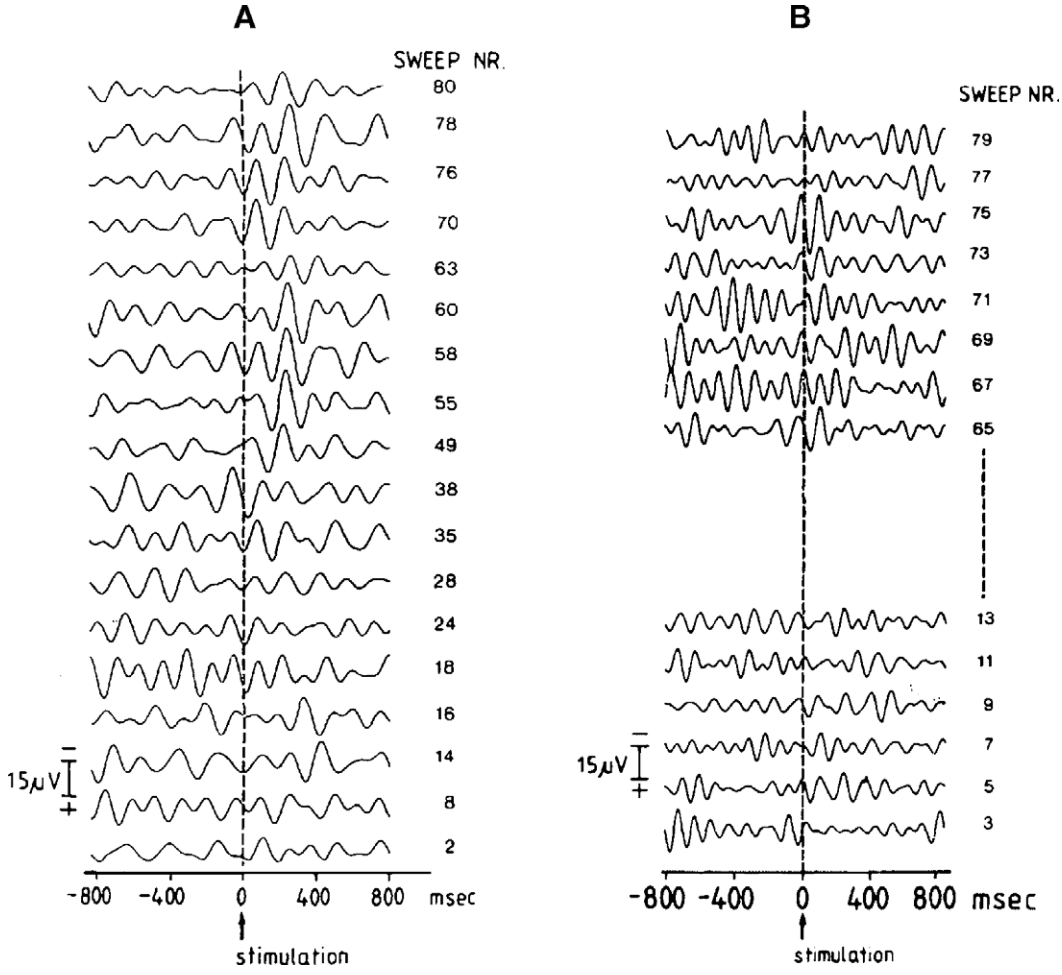

Fig. 11. (A) Filtered EEG-ERP epochs following randomly applied target tones are filtered in the 3.5- to 8-Hz frequency band. Sweeps 2 through 80 are shown. The prolonged and enhanced 3.5- to 8-Hz (theta) deflection is observed after Sweep 49. (B) Filtered EEG-ERP epochs to repetitively applied rate target tones. Filter limits are 8 to 13 Hz. Two groups of sweeps (3 through 13 and 65 through 79) are illustrated separately to show relevant changes in EEG and ERP activities. (Modified from Basar, E. and Stampfer, H.G., *International Journal of Neuroscience*, 26, 161, 1985).

LTM, at least for longer time intervals in comparison to working memory. Astonishingly, time periods of working memory and the duration of storage in the LTM are not clearly defined in the literature. In our opinion, we should better introduce the expression "*longer acting memory*" instead of long-term memory in order to show the differentiation to working memory and *persistent memory.*

The next step in the hierarchy of the memories of Fig. 6 is the transition of memory traces acquired in all day experience–and is temporarily stored in *longer acting memory*–to *persistent memory*. According to memory levels described in Fig. 6, the persistent memory includes the inborn memory as the physiological memory (being an ensemble of sub-memories as echoic memory, iconic memory, olfactory memory, etc.) and of the stabilized parts of *longer acting memory* acquired during the life. The question, how the new information acquired during processes of memory evolution or memory building (manifested with multiple oscillations and enhanced coherence in the whole brain), is transferred and stored in the persistent memory, surpasses the scope of the present book and remains yet unclear. However, it is important to indicate that the networks of the persistent memory operate with the same oscillatory dynamics of *evolving memory, i.e., by using the same basic oscillatory codes alpha, beta, theta, etc.* This indicates that possibly frequency codes are also transferred to persistent memory, or the frequency codes play an essential role during the transition. They are probably *invariant building blocks also partly contributing to the development of memory traces* (or engrams) in which the principle of *susceptibility* plays a major facilitation of signal transfer. According to Tranel and Damasio (1995), there is good reason to believe that depending on the type of memory under consideration, the storage may be *selectional or instructional*—i.e. it may depend more or less on selection from a pre-existing repertoire of neuron circuit states (cf. Edelman, 1987; Shenoy et al., 1993).

9. Super-synergy in the whole brain

The super-synergy comprehends an ensemble of at least 7 mechanisms that act in synergy upon sensory–cognitive input. It is proposed that the coexistence and cooperative action of these interwoven and interacting sub-mechanisms is a manifestation of integrative brain functions.

In the following, these interacting sub mechanisms are shortly described:

1. The *superposition principle* that includes the alpha, beta, gamma, theta and delta bands (Başar et al., 1999a,b,c; Chen and Hermann, 2001; Karakaş, 1997; Klimesch et al., 2000a,b);
2. *Activation of more than one type of selectively distributed oscillations in gamma, alpha, theta and delta bands* upon exogenous or endogenous input. These activities are manifested with a multifold occurrence of parameters such as *enhancement, delay, blocking (resynchronization), and prolongation* (Başar, 1980, 1999; Başar et al., 1999a,b,c, 2000, 2001a,b,c,d);
3. *Temporal and spatial changes of entropy* in the brain (Quiroga et al., 1999; Rosso et al., 2001, 2002);
4. *Temporal coherence between cells in cortical columns* for simple binding (Eckhorn et al., 1988; Gray and Singer, 1989);
5. *Varying degrees of spatial coherence* that occur over long-distances as parallel processing (Başar, 1980, 1983a,b; Başar et al., 1999a,b,c; Kocsis et al., 2001; Miltner et al., 1999; Schürmann et al., 2000);
6. *The relation between EEG and* event-related *oscillations, prestimulus EEG as a control parameter for brain responsiveness* (Başar et al., 1998; Barry et al., 2003a,b);
7. Complex matching in the whole brain (see Fig. 10A, B).

Thus, integrative brain function can be described as a *spatio-temporal organization.* The principle of superposition describes integration over the temporal axis, consisting of temporal relationship between the amplitude and phase of oscillations in various frequency bands. Furthermore, selectively distributed and selectively coherent oscillatory activity in neural populations describe integration over the spatial axis. Consequently, integrative activity is a function of the coherences between spatial locations of the brain; these coherences vary according to the type of sensory and or cognitive event and possibly the state of consciousness of the species.

The empirically founded sub-mechanisms are accompanied by the formation of a percept or in general of all cognitive events. This is realized through combinations of the response parameters among which are the varying strengths in the associative links between brain structures. The number of possible combinations can lead to an enormous amount of neuroelectric configurations. Spatio-temporal and functional organization of multiple and distributed oscillations in the brain inevitably lead to superbinding as a way to explain the integrative activity of the brain during the formation of percepts and other cognitive events.

We denote tentatively "*superbinding*" the combination of mechanisms of *superposition*, *activation of selectively distributed oscillatory systems* and *the selectively distributed long-distance coherence*. Because, superbinding reflects binding over long distances and also superposition of oscillations in the whole brain. This means that oscillations in multiple frequency windows in widely distributed areas in the brain are acting in concert. They are coupled and superimposed. There is an enormous synergy in the brain, in space and time.

Cooperation between cells was first outlined by Hebb (1949). Hebb's rule implies that information processing requires functional cooperations of distributed neurons. More exactly, this rule postulates that groups of synapses

converging on a single neuron and having the tendency to fire together will become strengthened as a group. This is the principle of cooperativity (Hebb, 1949). The distributed nature of activations in cognitive tasks, that are described in this report, possibly explain why Karl Lashley could have thought that the brain operates as a "*whole*." The cooperation between distributed structures of the brain can be weak or strong, since the coherences are selectively distributed. Parallel analysis of oscillations in several neural populations of the brain and in various frequency windows therefore brings a new refinement to the descriptions of the expressions "*the whole brain*" and the "*cooperativity*": The whole brain is activated in all perceptual and memory related mechanisms. The intensity of electrical oscillatory responses is selective in neural populations. The links or cooperativity, measured by means of coherences and phase differences, shows also varied degrees of intensities. Accordingly, we possibly may talk about new interpretations of Lashley's and Hebb's statements by using all these new tools to analyze the electrical activity of the brain during sensory–cognitive processes.

10. Conclusion

Leitmotivs, strategies, and concluding remarks of this paper are:

1. The machineries of super-synergy in the whole brain are responsible for formation of sensory–cognitive percepts.
2. The expression "*dynamic memory*" is used for memory processes that evoke relevant changes in alpha, gamma, theta and delta activities. The concerted action of distributed *multiple oscillatory processes* provides a major key for understanding of *distributed memory*. It comprehends also the phyletic memory and reflexes.
3. The evolving *memory*, which incorporates reciprocal actions or reverberations in the *APLR alliance* and during *working memory processes*, is especially emphasized.
4. A new model related to "*hierarchy of memories as a continuum*" is introduced.
5. The notions of "*longer activated memory*" and "*persistent memory*" are proposed instead of long-term memory.
6. The new strategy to recognize faces emphasizes the importance of EEG oscillations in neurophysiology and Gestalt analysis.
7. According to Damassio (1997) memory depends on several brain structures working in concert across many levels of neural organization*; memory is a constant work-in progress*." The proposition of a brain theory based on super-synergy in neural populations is most pertinent for the understanding of this constant work in progress.
8. The proposed basic framework called "*memory in the whole brain work*" emphasizes that memory and all brain functions are inseparable and are acting as a "*whole*" in the whole brain.
9. A link from the "*whole brain*" to "*whole body*," and incorporation of vegetative and neurological system is proposed, EEG oscillations and ultraslow oscillations being a control parameter.

Anatomical abbreviations

GEA	*Gyrus ectosylvian anterior, auditory cortex*
MG	*Medial geniculate nucleus*
LG	*Lateral geniculate nucleus*
IC	*Inferior Colliculus*
HI	*Hippocampus*
OC	*Occipital cortex, area 17*
RF	*Reticular formation*
SC	*Superior colliculus*
CA3	*Ca3 layer in hippocampus*:
IC	*Inferior Colliculus*
SC	*Superior colliculus*
CE	*Cerebellum*

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